

Improving Estimation of Wolf Recruitment and Abundance, and Development of an Adaptive Harvest Management Program for Wolves in Montana



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INTRODUCTION

Wolves (*Canis lupus*) were reintroduced into 2 areas in the southern portion of the northern Rocky Mountains (NRM) in 1995, and after rapid population growth were delisted from the endangered species list in 2011. Since that time, states in the NRM have agreed to maintain populations and breeding pairs (a male and female wolf with 2 surviving pups by December 31; USFWS 1994) above established minimums (≥ 150 wolves and ≥ 15 breeding pairs within each state). Montana estimates population size every year using patch occupancy models (POM; Miller et al. 2013; Rich et al. 2013; Bradley et al. 2015), however, these estimates are sensitive to pack size and territory size, and were developed pre-harvest. Reliability of future estimates based on POM will be contingent on accurate information on territory size, overlap, and pack size, which are expected to be strongly affected by harvest. Additionally, breeding pairs, which has proven to be an ineffective measure of recruitment, are determined via direct counts. Federal funding for wolf monitoring has ended in states where wolves are delisted, and future monitoring will not be able to rely on intensive counts of the wolf population. Furthermore, intensive, field-based monitoring has become cumbersome and less effective since the population has grown. With the implementation of harvest, predicting the effects of harvest on the wolf population and continuing to monitor the effectiveness of management actions is required to make informed decisions regarding hunting and trapping seasons.

STUDY OBJECTIVES

Our 4 study objectives are to:

1. Improve estimation of recruitment.
2. Improve and maintain calibration of wolf abundance estimates generated through POM.
3. Develop a framework for dynamic, adaptive harvest management based on achievement of objectives 1 & 2.
4. Design a targeted monitoring program to provide information needed for robust estimates and reduce uncertainty in the AHM paradigm over time.

Two PhD students are addressing the 4 study objectives as part of Project 1 (Sarah Sells) and Project 2 (Allison Keever; Fig. 1).

DELIVERABLES

1. A method to estimate recruitment for Montana's wolf population that is more cost effective and biologically sound than the breeding pair metric (Project 2, A. Keever).

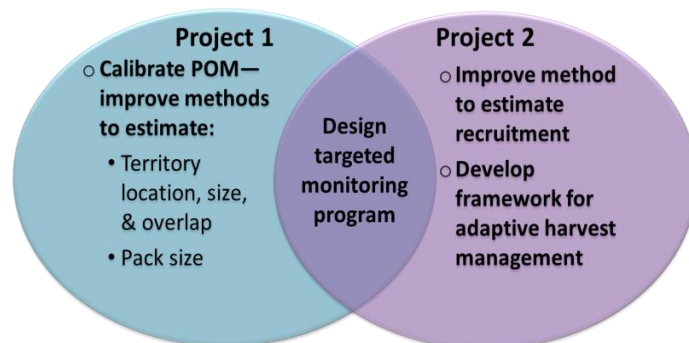
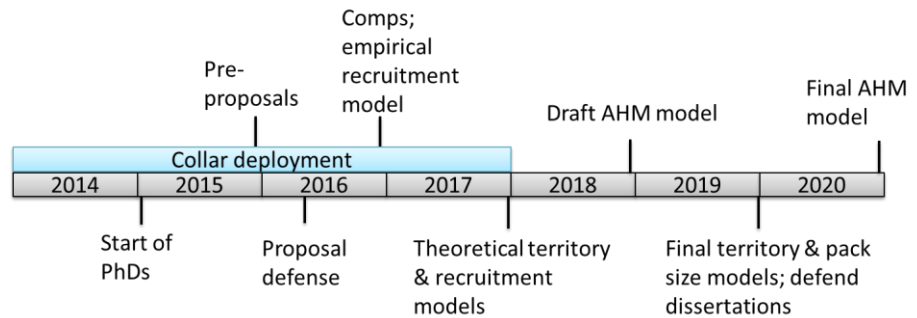


Fig. 1. Objectives for this project are being addressed under 2 separate projects.

- Models to estimate territory size and pack size that can keep POM estimates calibrated to changing environmental and management conditions for wolves in Montana (Project 1, S. Sells).



- An adaptive harvest management model that allows the formal assessment of various harvest regimes and reduces uncertainty over time to facilitate adaptive management of wolves (Project 2, A. Keever).
- A recommended monitoring program for wolves to maintain calibration of POM estimates, determine effectiveness of management actions, and facilitate learning in an adaptive framework (Projects 1 & 2).

Fig. 3. Project timeline.

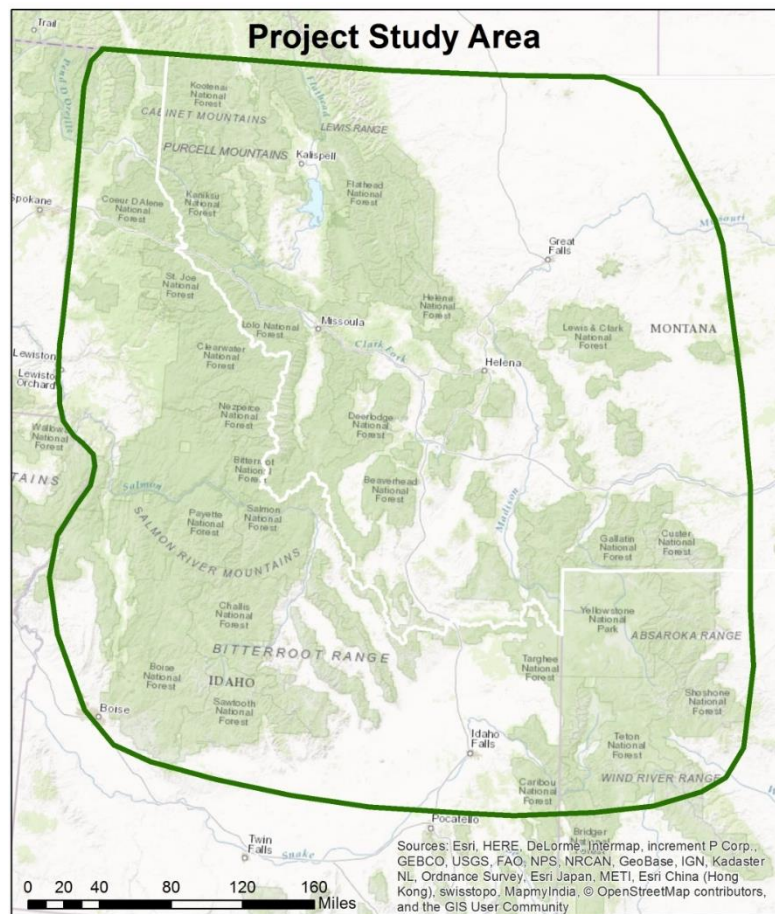


Fig. 2. The project study area includes wolf distribution in Montana and Idaho, as well as Yellowstone.

LOCATION

This study encompasses wolf distribution in Montana and Idaho (Fig. 2). Additional data will come from Yellowstone National Park for the territory models developed under objective 2.

GENERAL PROGRESS

Projects 1 & 2, Year 1: We (S. Sells & A. Keever) started our PhD programs in January 2015 (Fig. 3). Much of year 1 was devoted to literature reviews on animal behavior, carnivores, modeling, optimal foraging, etc. and determining approaches for the dissertations. We also formed and held multiple

meetings with our committees, worked on completing coursework requirements, and finalized research statements. Additional efforts focused on communicating with wolf specialists, identifying target packs for collaring, managing collar orders and data, and helping coordinate contracts and capture plans for winter aerial captures for January and February 2016. We also met with wolf specialists in the field to learn more about the wolves in each region, and coordinated and held meetings with the specialists to plan future project efforts.

Project 1 (S. Sells): In year 2, I continued most activities from year 1, including conducting literature searches, taking classes, holding committee meetings, communicating with wolf specialists, managing collar orders, managing data, etc. I also began working on the theoretical territory models. My primary focus was meeting project and university requirements and deadlines, including defending my proposal and passing my comprehensive exams. I also joined the wolf specialists to assist with a month of trapping.

Year 3 was primarily devoted to preparing the theoretical territory models. I presented draft results at 5 conferences. In addition to completing more coursework, I continued working with MFWP and collar manufacturers as the point person on ordering collars, troubleshooting a growing set of issues with the collars, and managing collar records. I continued coordinating data management and collection from deployed collars and communicating with wolf specialists on all trapping and collar-related topics. I also spent 2 weeks assisting wolf specialists with trapping.

In Year 4, I finalized the first-generation theoretical territory model and prepared drafts of the related manuscript for future publication. I attended an international training to learn the final steps for preparing and using individual-based models, which provide the foundation of my work. I also presented results at a national conference in the fall. I completed several steps towards building empirical territory models by preparing data, writing code, estimating territory sizes and locations for GPS-collared wolves from 2008 – 2018, and running univariate analyses. I also completed work towards parameterizing the theoretical territory model; the outcome of this stage will be used to calibrate POM. I continued managing and adding to the wolf database for this project (including all GPS locations and their attributes), which will be sent to MFWP upon project completion. As in earlier years, I continued to serve as the point person for collar-related tasks, and spent 2 weeks assisting MFWP wolf specialists with trapping. I also completed my teaching requirements at the University by independently teaching an undergraduate course.

Project 2 (A. Keever): In year 2 I continued literature reviews, completed coursework, and meeting university requirements. I defended my proposal and was studying for my comprehensive exams. Another focus was on the empirical recruitment model. I began developing the model that I had outlined in my proposal. I also spent 1 month assisting wolf specialists with trapping.

Year 3 I completed the empirical recruitment model code and tested the model with simulated data. Much of my time was spent compiling and formatting the data needed to estimate recruitment. I presented preliminary results at 2 conferences. I also passed my comprehensive exams and spent 2 weeks assisting wolf specialists with trapping.

In Year 4 I completed the empirical recruitment models and prepared drafts of the manuscript for future publication. I completed a simulation study to test the empirical recruitment model and evaluate data

requirements. I began working on a draft manuscript of the simulation study for future publication. I began working on drafts of the theoretical recruitment models. I met with wildlife managers, area biologists, wolf specialists, and supervisors for each of the regions with wolves to determine objectives and alternative actions (harvest regulations) for wolf management. Additionally, I provided code for a Bayesian patch occupancy model to facilitate abundance estimation in the current POM framework. I completed teaching requirements for the University and spent 2 weeks assisting wolf specialists with trapping.

Deliverables and updates: Project deliverables will include an empirical recruitment model; theoretical territory, group size, and recruitment models; draft and final AHM models; and final territory and pack size models. Additionally, it was agreed in 2017 that Project 1 would also provide empirical territory and group size models. We have been working on deliverables of the empirical recruitment model, theoretical recruitment model, and adaptive harvest management model (A. Keever) and the theoretical and empirical territory models (S. Sells) towards meeting objectives 1, 2, and 3. We each describe our progress towards these deliverables in subsequent sections of this report. (Additional details on objective 4 are available in the 2016 report.)

ACKNOWLEDGEMENTS

This project would not be possible without the generous assistance of biologists and managers at Montana Fish, Wildlife and Parks, including Abby Nelson, Ty Smucker, Kent Laudon, Tyler Parks, Nathan Lance, Mike Ross, Diane Boyd, Molly Parks, Brady Dunne, Liz Bradley, Jessy Coltrane, Kelly Proffitt, John Vore, Quentin Kujala, Neil Anderson, and Bob Inman. Biologists and managers at Idaho Fish and Game also provide generous assistance, including David Ausband and Mark Hurley. We also thank landowners for allowing access for trapping and collaring efforts. Additionally, faculty and staff at the University of Montana provide invaluable support.

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PROGRESS ON OBJECTIVES

OBJECTIVE 1: IMPROVE ESTIMATION OF RECRUITMENT—*Allison Keever, Project 2*

1.1 Introduction

Estimating recruitment (i.e., number of young produced that survive to an age at which they contribute to the population) of wolves is difficult because the size of the wolf population and limited time and funding for monitoring. Currently, MFWP documents recruitment based on visual counts of breeding pairs (a male and female wolf with 2 surviving pups by December 31; U.S. Fish and Wildlife Service 1994). These counts, however, are incomplete due to the large number of wolves in the population. Additionally, now that states fund their own monitoring programs, future monitoring will not be able to rely on intensive counts.

Recruitment in wolves can depend on their social structure. Wolves are cooperative breeders, and pack dynamics (e.g., pack tenure, breeder turnover, and number of non-breeding helpers) can affect recruitment through pup survival (e.g., Ausband et al. 2015). Cooperative breeding often relies on the presence of non-breeding individuals that help raise offspring (Solomon and French 1997), and reduction in group size can lead to decreased recruitment in cooperative breeders (Sparkman et al. 2011; Stahler et al. 2013). Human-caused mortality through both direct and indirect means (Ausband et al. 2015) and prey biomass per wolf (Boertje and Stephenson 1992) have been shown to affect recruitment. As a result, it will be important to consider the effects of harvest, pack dynamics, wolf density, and prey availability on recruitment.

Existing monitoring efforts yield insufficient data to estimate recruitment using traditional methods; therefore a new approach is needed that does not rely on extensive data. A breeding pair estimator (Mitchell et al. 2008) could be used to estimate breeding pairs, but requires knowledge of pack size; such data are hard to collect given the size of the wolf population. Additionally, the breeding pair metric is an ineffective measure of recruitment because it provides little insight into population growth rate or the level of harvest that could be sustained. Recruitment could be estimated by comparing visual counts at the den site to winter counts via aerial telemetry (Mech et al. 1998) or by marking pups at den sites (Mills et al. 2008). An alternative method could include non-invasive genetic sampling (Ausband et al. 2015) at predicted rendezvous sites (Ausband et al. 2010). These methods, however, may not be feasible on large scales due to budget and staff constraints.

1.2 Sub-Objectives of Objective #1

Developing methods to estimate recruitment with limited data relies on meeting 3 sub-objectives:

- 1. Develop and test an empirical recruitment model.**
 - a. Test accuracy and precision of estimates generated by model.
 - b. Provide understanding of how the social structure of wolves affects demography and estimation of recruitment.
 - c. Evaluate data requirements of the method.
- 2. Estimate recruitment of wolves in Montana.**
 - a. Provide estimates that are more biologically credible than breeding pair metric.

- b. Improve understanding of variation in recruitment.
- 3. Develop and test theoretical models for recruitment.**
 - a. Reduce need for data to estimate recruitment.
 - b. Improve understanding of variation in components of recruitment.

1.3 General Approach

We will develop an empirical recruitment model (hereafter ERM) using the framework of an integrated population model. Integrated population models can be a useful tool for demographic analyses from limited datasets, and can increase precision in estimates (Besbeas et al. 2002). Our goal is to estimate recruitment and evaluate factors that may cause spatial and temporal variation in recruitment. Our goal is also to conduct a simulation study to evaluate how many data are needed to reliably estimate recruitment.

We will also develop theoretical models of recruitment to evaluate factors that cause variation in the components of recruitment. Recruitment depends on a pack's success in breeding and giving birth, litter size, pup survival, and the number of breeders in a pack. We will use the theoretical models to test hypotheses about factors that affect the components of recruitment and produce predictions of patterns we would expect to see in recruitment of wolves.

1.4 Develop and Test Empirical Model: Sub-Objective #1

Introduction

We used an integrated population model framework to estimate recruitment with limited data. Integrated population models generally use time-series count data to inform changes in abundance over time, mark-recapture data to inform survival, and survey data to inform recruitment (Abadi et al. 2010; Schaub and Abadi 2011). With an integrated population model it is possible to estimate recruitment with only survival and count data, because changes in abundance over time contain information on changes in vital rates.

Further, we adapted the integrated population model to account for the social structure of wolves. Traditional integrated population models inherently ignore social structure which can greatly affect demography (Al-Khafaji et al. 2009). For wolves, the population is a collection of packs and the packs themselves are a collection of individuals. Within a pack, wolves can survive, disperse, or be recruited. Packs similarly can go extinct (e.g., dissolve) and new packs can be formed. The processes that occur within a pack (e.g., dispersal) can affect the processes that occur among packs (e.g., pack formation).

We conducted a simulation study to determine whether the ERM would be useful to estimate recruitment of wolves. For the model to be useful for monitoring wolves in Montana it needs to produce accurate estimates and require less field data (e.g., group counts and collars). The benefit of a simulation study is that we know the true number of wolves and their demographic rates, allowing us to compare estimates from the model to truth to assess accuracy. We also determined the accuracy of estimates with decreasing amounts of group count and collar data (i.e., considering a similar amount of data as collected in the past and less).

Methods

Model structure

We developed an ERM to estimate recruitment of wolves in Montana and evaluate factors causing spatial and temporal variation. To account for social structure of wolves we modeled the processes that occur within packs and the processes that occur among packs (Figure 1.1). We used 1)

estimates of abundance from POM to inform changes in abundance over time, 2) estimates of colonization and extinction from POM to inform group formation and extinction, 3) group counts to inform changes in pack size over time, 3) GPS and VHF collar data to estimate survival, and 4) data from the literature to model dispersal (Jimenez et al. 2017). We ignored adoption of individuals into the pack because we assumed it was rare. Recruitment was the only parameter without data and could therefore be estimated.

We used POM (MacKenzie et al. 2002; Miller et al. 2013; Rich et al. 2013) to estimate the area occupied by wolves and colonization and extinction rates. Using the mean territory size estimated by Rich et al. (2012) in 2008–2009, we estimated the number of packs by dividing area occupied by mean territory size. We estimated mean group size based on group count data (MFWP 2018), and multiplied mean group size by the number of packs to estimate abundance. Eventually, models from Objective 2 (territory and group size) could also be incorporated to improve estimates of abundance in the model.

We estimated survival using a discrete-time proportional hazards model with a complementary log-log (cloglog) link function. We used 4 discrete periods for analyses: the denning period (April-May), rendezvous period (June-August), the hunting-only period (September-November), and the hunting/trapping period (December-March). GPS and VHF collared adult and yearling wolves from 2007–2016 provided the known-fate data needed to estimate survival. We did not include wolves that were removed for livestock depredation in survival analysis as these have inherent sampling bias. We included a random year effect on survival to account for yearly variation.

We modeled recruitment as the number of pups per pack using generalized linear models with a log link function. The linear predictor could then be described using covariates to test hypotheses about factors influencing recruitment. For the simulation study we included a random effect of year to account for annual variation.

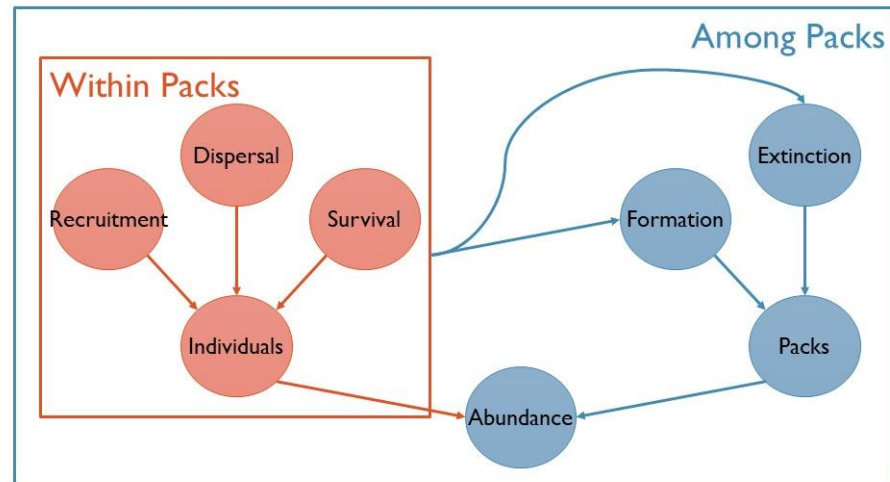


Figure 1.1. Diagram of ERM model structure for wolves that accounts for the hierarchy of demography in wolf population dynamics. Blue circles represent processes that occur among packs and red circles represent processes that occur within packs.

Data simulation

We simulated a wolf population for 15 years and then sampled from the population. We first generated 100 wolf packs with group counts using a Poisson distribution with an average pack size of 7 wolves. We then randomly generated survival, recruitment, and dispersal rates using a uniform distribution with a range of biologically realistic rates for each year (Murray et al. 2010; Smith et al. 2010; Ausband et al. 2015; Stenglein et al. 2015). This allowed for yearly variation in the demographic rates, which we recorded as truth. The simulated wolves in the initial 100 packs survived and reproduced based on these demographic rates. We included stochasticity using a Poisson distribution for reproduction and a binomial distribution for survival and dispersal. The number of packs was determined by generating random patch occupancy, colonization, and extinction rates from biologically realistic rates for each year and calculating the area occupied by wolves. We divided the area occupied by wolves by 600km² (Rich et al. 2012) to determine the number of packs for our truth to compare estimates to.

We sampled group count data and estimates of mean group size from these packs. We added up the number of individual wolves in the packs to calculate true total abundance. We sampled from the individual wolves to create the collar datasets. We used different amounts of data from the simulated population to evaluate the amount of data needed to get reliable estimates of recruitment. For group counts we randomly sampled 50 packs per year, which represented the maximum amount of data collection that field biologists could realistically do each year (K Podrutzny, pers. comm.). Additionally, we randomly sampled 25 and 12 packs per year to create datasets representing reduced monitoring effort. We added observation error to these counts so that the data were also a sample of wolves within the pack.

Because the goal of MFWP is to expend less field effort for wolf monitoring, we also tested the model without any group data. This yielded 4 total datasets (50, 25, 12, and 0 pack counts per year). For collar data we sampled 50, 20 and 10 wolves per year to generate known-fate observations. We then sampled and created datasets for 20 and 10 collars every year, every 2 years, and every 5 years (6 datasets). We used every combination of the collar and group count datasets for a

Table 1.1. Mean percent error and standard deviation of estimates from an integrated population model for recruitment (γ), mean group size (G), abundance (N), and survival (ϕ) from truth for a simulated wolf population with different amounts of collar and group count data. For number of collars it is the mean from all group count datasets and for group counts it is the mean from all collar datasets.

Number of collars	$\bar{\gamma}$ (SD)	\bar{G} (SD)	\bar{N} (SD)	$\bar{\phi}$ (SD)
10	29.5% (22.90%)	5.7% (3.05%)	9.9% (8.23%)	8.6% (6.46%)
10 every 2 years	30.6% (26.35%)	5.7% (3.05%)	9.7% (8.02%)	11.3% (8.41%)
10 every 5 years	55.1% (28.99%)	5.8% (3.06%)	8.9% (7.05%)	31.6% (21.58%)
20	27.8% (22.08%)	5.7% (3.05%)	9.3% (7.95%)	8.1% (6.05%)
20 every 2 years	30.7% (21.41%)	5.7% (3.05%)	9.4% (7.98%)	10.1% (6.97%)
20 every 5 years	63.7% (29.36%)	5.8% (3.05%)	8.6% (7.68%)	36.3% (22.01%)
Group Counts				
0	54.5% (33.27%)	NA	15.9% (7.81%)	20.0% (18.64%)
15	39.8% (29.75%)	5.8% (3.33%)	7.3% (7.36%)	19.5% (20.16%)
25	40.8% (26.53%)	5.5% (3.15%)	6.7% (5.60%)	21.0% (20.13%)
50	23.2% (13.78%)	5.9% (2.55%)	7.2% (6.16%)	10.2% (8.61%)

total of 24 scenarios. For each scenario we generated occupancy data by sampling 500 sites with 5 occasions per year. We did not evaluate the amount of occupancy data needed to provide reliable estimates because those data are relatively inexpensive to collect and those methods have been used by MFWP since 2007.

We estimated recruitment using the model for all 24 scenarios. We compared estimates of recruitment to truth and calculated the percent error for each of the scenarios. We used Markov chain Monte Carlo (MCMC; Brooks 2003) methods in a Bayesian framework to fit the ERM using program R 3.4.1 (R Core Team 2017) and package R2Jags (Su and Yajima 2015) that calls on program JAGS 4.2.0 (Plummer 2003). We ran 3 chains for 100,000 iterations. We discarded the first 50,000 iterations as a burn-in period and used a thinning rate of 2.

Results and Discussion

The models for all scenarios using group count data converged and had Gelman-Rubin statistics < 1.1 for each parameter. The scenarios with 50 group counts were most accurate in estimating recruitment across collar datasets, and scenarios with 25 and 15 group counts were comparable in accuracy of estimating recruitment across collar datasets (Table 1.1). Recruitment estimates with 15 and 25 group counts and 20 or 10 collars at least every 2 years were similar to recruitment estimates with 50 group counts and the same collar data (Figure 1.2). Models for scenarios without group count data (not accounting for social structure) had trouble converging, and those that did converge were less precise and accurate than scenarios with group counts. Survival estimates for scenarios with 10 or 20 collars at least every 2 years were accurate for all amounts of group count data, and survival estimates were only inaccurate for 10 or 20 collars every 5 years and 25 group counts or less (Figure 1.3). Estimates of abundance were similarly accurate for all scenarios, however the scenarios without group counts were less precise.

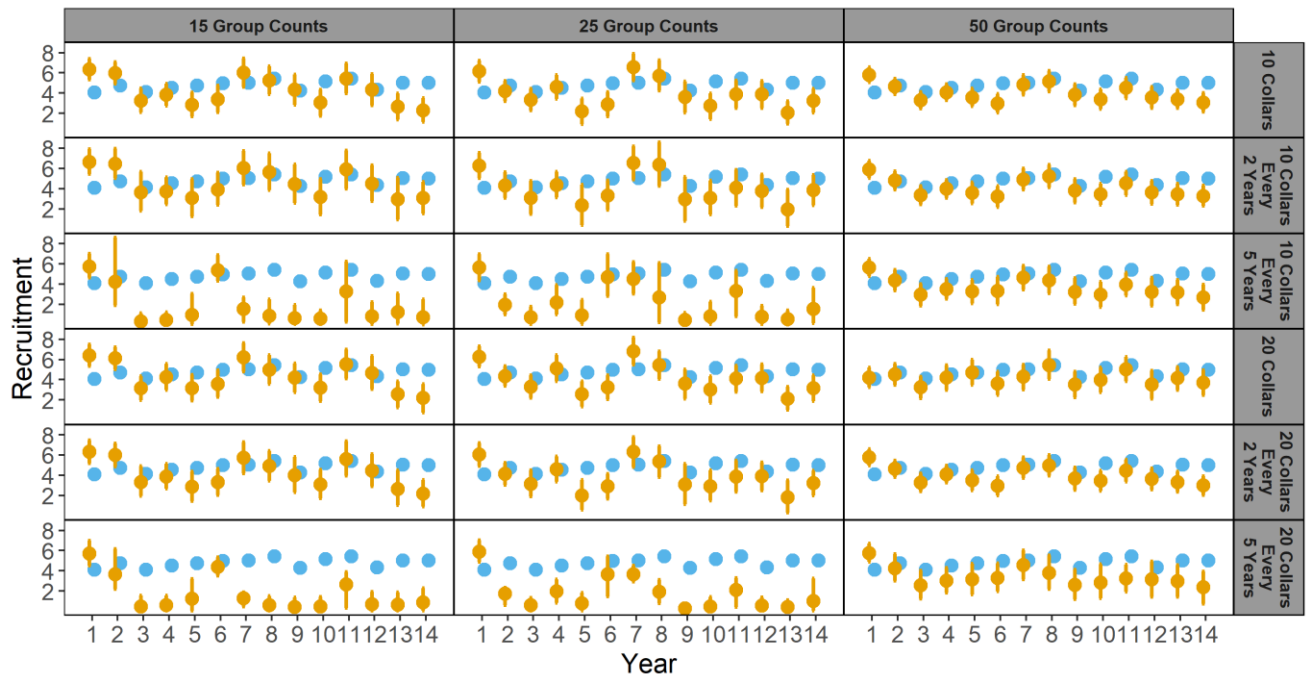


Figure 1.2. Estimates of recruitment in number of pups per pack that survive 1 year (orange circles) from an integrated population model compared to truth (blue circles) for a simulated wolf population with different amounts of group count and collar data.

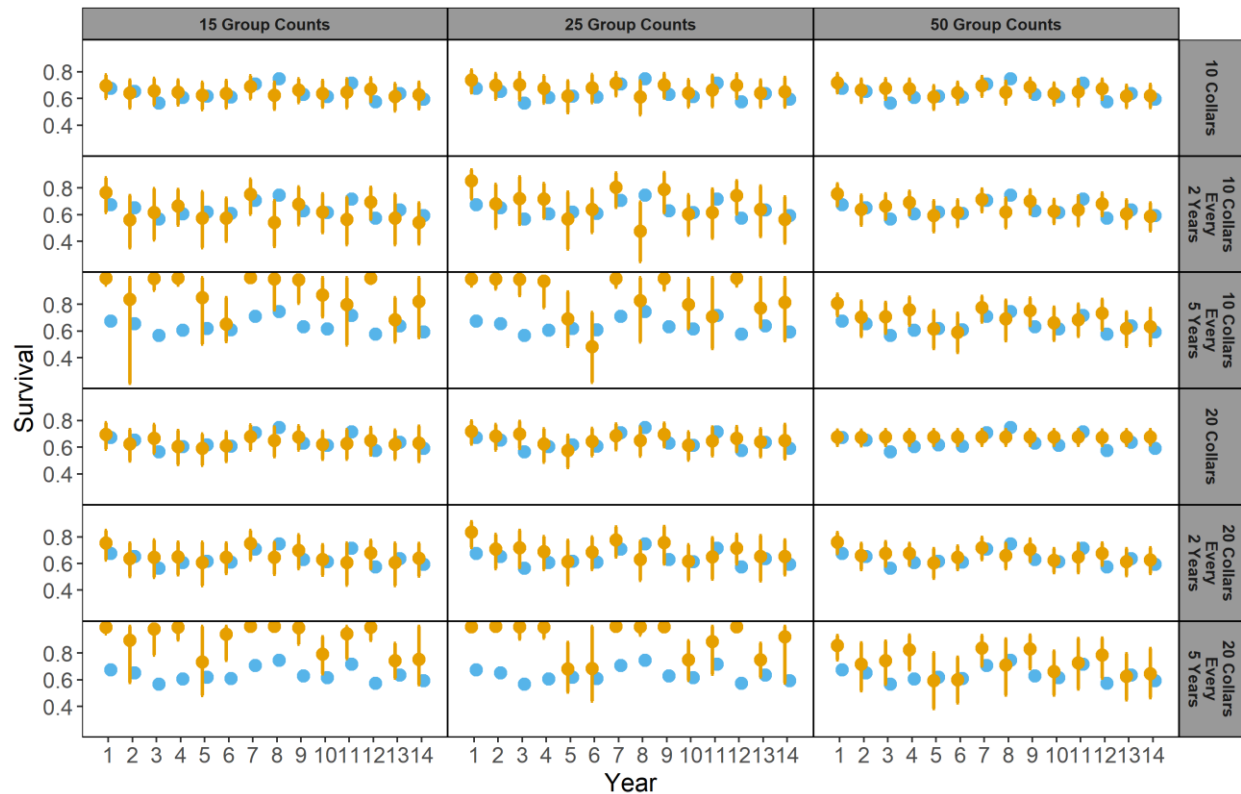


Figure 1.3. Estimates of survival (orange circles) from an integrated population model compared to truth (blue circles) for a simulated wolf population with different amounts of group count and collar data.

Given our goal was to provide a method to estimate recruitment that is both biologically credible and cost effective, a main determinant of success would be the amount of data required. Simulations suggest that the ERM can be a viable method to estimate recruitment; however group count data greatly increase the precision and accuracy of estimates. There appears to be little benefit (accuracy of estimates) to increase monitoring efforts from 10 collars every 2 years and 15 group counts to 1) 20 collars every 2 years or 2) 10 or 20 collars every year. Similarly, there appears to be little benefit (accuracy of estimates) to increase monitoring from 15 group counts and 10 collars every 2 years to 25 group counts with the same collar data. There was an increase in accuracy, however, with 50 group counts. As part of meeting deliverable 4 (monitoring program), we will assess tradeoffs between resources spent collecting data and accuracy of estimates generated from those data. For example, accuracy is comparable between 10 collars every 2 years and 20 collars ever year with 15 group counts. Therefore, the difference in cost would determine the best option.

The other objective of this work was to provide a method that is more biologically credible than the breeding pair metric. The breeding pair metric estimates the probability a pack contains a breeding pair. Using the breeding pair metric a manager can determine how many packs recruited at least 2 pups and a minimum of recruitment, however the ERM can estimate the number of pups recruited per pack. Further, because the model was developed in a Bayesian framework we can estimate other derived quantities of recruitment such as the total number of pups recruited to the population. Future research could also evaluate the accuracy of these quantities of recruitment. We can also use the ERM to answer biological

questions about variation in the number of pups produced per pack to improve understanding of wolf population dynamics.

1.5 Estimate Recruitment in Montana: Sub-Objective #2

Introduction

Recruitment in wolves can be a driving factor of population growth. A pair of wolves that breeds produces an average of 4-6 pups per litter which can more than double the population (Fuller et al. 2003). Further, because pups tend to be the largest age class in the population (Fuller et al. 2003) future population size is mainly determined by pup recruitment. Variation in recruitment therefore can cause variation in population growth rate.

We evaluated how recruitment in wolves varied across Montana. We tested the hypothesis that variation in recruitment of wolves was driven by intrinsic factors. Intrinsic factors at the pack-level such as pack size and composition can affect recruitment of pups (Ausband et al. 2017a; Ausband 2018). The number of non-breeding helpers in a group influences recruitment of young in many species that cooperatively breed, including wolves (Solomon and French 1997; Courchamp et al. 2002; Stahler et al. 2013; Ausband et al. 2017a). Therefore, we predicted that recruitment would be positively correlated with pack size. An intrinsic factor that could affect recruitment is density. Conspecific aggression can negatively affect survival (Cubaynes et al. 2014), which could decrease recruitment of pups directly or indirectly and we predicted a decrease in recruitment with population size. Gude et al. (2012) and Stenglein et al. (2015b) found evidence of density-dependence in recruitment, and density may be an important intrinsic factor driving recruitment. Accordingly, we predicted that pack size or population density would explain most of the variation in recruitment.

Alternatively, we hypothesized that extrinsic factors drive variation in recruitment. If so, we predicted that winter severity, forest cover, road density, or harvest would explain most of the variation in recruitment. Forest cover is positively associated with occupancy of wolves (Rich et al. 2013; Bassing et al. 2018), and may be associated with security cover from humans (Llaneza et al. 2012). If so, we predicted that recruitment would increase with forest cover. A proxy for availability of prey could be winter severity. Winter severity (e.g., snow depth) increases the vulnerability of ungulates to predation by wolves (Huggard 1993; Post et al. 1999; Mech and Peterson 2003). Further, fluctuations in wolf populations have been linked, via fluctuations in prey, to fluctuations in winter severity (Peterson 1974; Mech et al. 1998; Mech and Fieberg 2015). If so, we predicted that winter severity would be positively correlated with recruitment. Harvest both directly and indirectly reduces recruitment (Ausband et al. 2015, 2017a), and it could cause significant spatial and temporal variation in recruitment if harvest varies spatially or over time. Spatial variation in harvest may be difficult to quantify, however road density could be used as a proxy for spatial risk of harvest. Although wolves avoid high-use roads (Thurber et al. 1994), low-use roads may be correlated with increased risk of harvest mortality by increasing access to hunters and trappers (Person and Russell 2008). We predicted that recruitment would decrease in years with harvest and in areas of increased road density.

Methods

We used the ERM to estimate and evaluate variation in recruitment of wolves in Montana. We used three datasets that were available from ongoing monitoring in Montana: hunter surveys, global positioning system (GPS) and very-high-frequency (VHF) collars, and group counts. We used hunter surveys representing detection/non-detection data to estimate occupancy of wolves from 2007-2017 (see Rich et al. [2013] and MFWP [2018] for details). We used data for adult and yearling wolves collected by VHF and GPS collars deployed by MFWP biologists from 2007-2017. Group counts were collected by MFWP biologists annually. We used the end-of-year group counts from MFWP (MFWP 2018) for wolves in Montana from 2007-2017 that the biologists considered complete (i.e., designated as “good quality”).

We classified low-use road density as either 4-wheel-drive or 2-wheel-drive roads (Rich et al. 2013; MFWP 2018) and calculated road density within a 600 km² buffer around the pack centroid, which represented average territory size of wolves (Rich et al. 2012, 2013). We removed roads in areas with human population densities > 25 people/km² because we assumed these represented high-use roads. We also calculated the proportion of the buffer covered by forest using ArcGIS (ESRI 2011). Forest cover was assessed by reclassifying 90 m² land cover pixels into forest and non-forest (Gap Analysis Project, Wildlife Spatial Analysis Lab, University of Montana). Data for forest cover and road density were from 2013, and we assumed this varied little over time. Harvest was a binary variable that was 1 in years with harvest and 0 in years without harvest. For winter severity we used the average daily snow depth for the previous water year (October 1 – September 30 the following year) from SNOTEL

(<https://www.wcc.nrcs.usda.gov/snow/>). We used the log of estimated population size and pack size. We also included a random effect for the FWP region of the pack centroid and a random effect of year as covariates to account for additional spatial and temporal variation. We had 2 candidate models that represented the intrinsic hypothesis and 4 candidate models that represented the extrinsic hypothesis (Table 1.2), and selection was based on posterior deviance. We only considered univariate models because we did not have recruitment data and did not want to over-parameterize the model. We repeated analyses as detailed above to estimate recruitment for wolves in Montana. We ran 3 chains for 100,000 iterations with the first

50,000 discarded as a burn-in period and a thinning rate of 3. We monitored convergence using visual inspection of the MCMC chains and the Gelman-Rubin diagnostic (Gelman and Rubin 1992). All results are presented with mean and 95% credible intervals unless otherwise specified.

Results and Discussion

A total of 114 adult and yearling wolves (63

Table 1.2. Deviance statistics (mean and standard deviation) and number of parameters (K) used for model selection to estimate recruitment of wolves in an integrated population model and test 2 alternative hypotheses. We tested the hypothesis that recruitment in wolves was driven by intrinsic factors such as density-dependence (population size) or pack size. Alternatively we hypothesized that recruitment was driven by extrinsic factors including years with and without harvest, proportion of territory with forest cover, snow-depth for the previous water year, and density of low-use, 4-wheel drive and 2-wheel drive roads within the territory. Lower deviance suggest more model support, and we considered those within a SD of the top model to have support.

Model	Hypothesis	K	Mean	SD
$\gamma \sim \text{Population Size} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Intrinsic	4	21021.12	163.65
$\gamma \sim \text{Pack Size} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Intrinsic	4	21025.56	162.31
$\gamma \sim \text{Harvest} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Extrinsic; human	5	21026.36	162.51
$\gamma \sim \text{Forest} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Extrinsic; prey	4	21642.61	162.51
$\gamma \sim \text{Snow} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Extrinsic; prey	4	21920.63	1265.98
$\gamma \sim \text{Roads} + \tau_{\text{Year}} + \tau_{\text{Region}}$	Extrinsic; human	5	22247.85	167.08

females and 51 males) were collared from 2007 – 2016 that were not removed for livestock depredation. The wolves were captured in 72 unique packs with an average of 1.58 (SD=1.58) collared wolves per pack. Of these wolves, 49% were adults and 36% were yearlings. The age class of the remaining 15% was unknown. The number of collared wolves per year ranged from 14 in 2007 to 48 in 2016. Of the 114 collared wolves, 46 had an unknown fate and were censored the time period of their last known location. Of those that were censored, 11% had the collar drop off and 22% had collar failure. The leading cause of death for the 50 wolves with documented mortality was legal harvest (n=24), followed by poaching (n=8). The remaining mortality was other human-caused mortality (n=6), natural mortality (n=6), and unknown cause of mortality (n=6). The average number of months a wolf survived was 24.2 (SD=11.74), and ranged from 2.2 – 67.4 months.

We excluded 527 group count observations (44.2%) of the original group count dataset because they were not classified as “good” or “moderate” quality by MFWP biologists. The final dataset included 664 group count observations from 217 packs, 2007-2016. The mean observations per year was 66.4 (SD=18.1, range=34–94). On average, each pack had 3.09 observations (SD=2.13), with 1 pack contributing 10 observations (i.e. 10 years of good or moderate quality counts). Average pack size for the 10 years was 5.7 (SD=2.91), and ranged from an average pack size of 4.96 (SD=2.24) in 2016 to 7.03 (SD=3.13) in 2007. During the period when wolves were listed under the ESA (2007-2008, 2010) average pack size was 6.6 (SD=3.30; n=139), and during the delisted period (2009, 2011-2016) average pack size was 5.5 (SD=2.76; n=525).

All models converged, with Gelman-Rubin statistics of <1.1 for all parameters. Parameters with Gelman-Rubin statistics close to 1.1 had good mixing of chains with visual inspection of diagnostic plots. The model with the lowest mean deviance included a density-dependent effect (Table 1.2). Population size had a positive effect on recruitment. Two competing models were within the standard deviation of the top model: 1) pack size and 2) harvest. Pack size had a slight negative effect on the number of pups recruited per pack, however the effect size was small. There was a > 95% probability that population size decreased recruitment and >

95% probability that pack size increased recruitment. There was an 88% probability that harvest had a negative effect on recruitment.

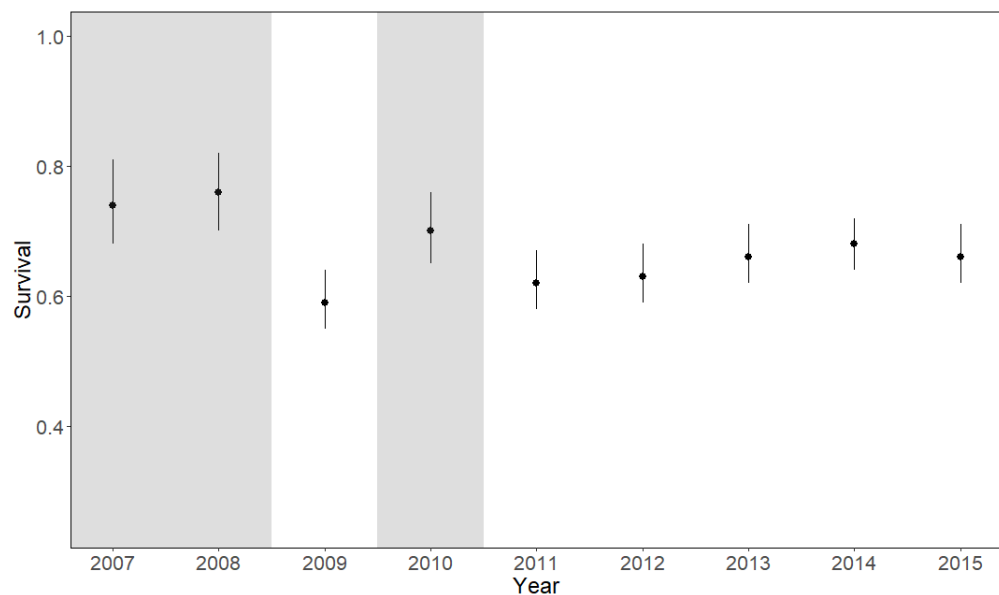


Figure 1.4. Estimates and 95% credible intervals of survival for adult and yearling wolves in Montana from 2007-2016. Shaded areas on the graph represent years without harvest.

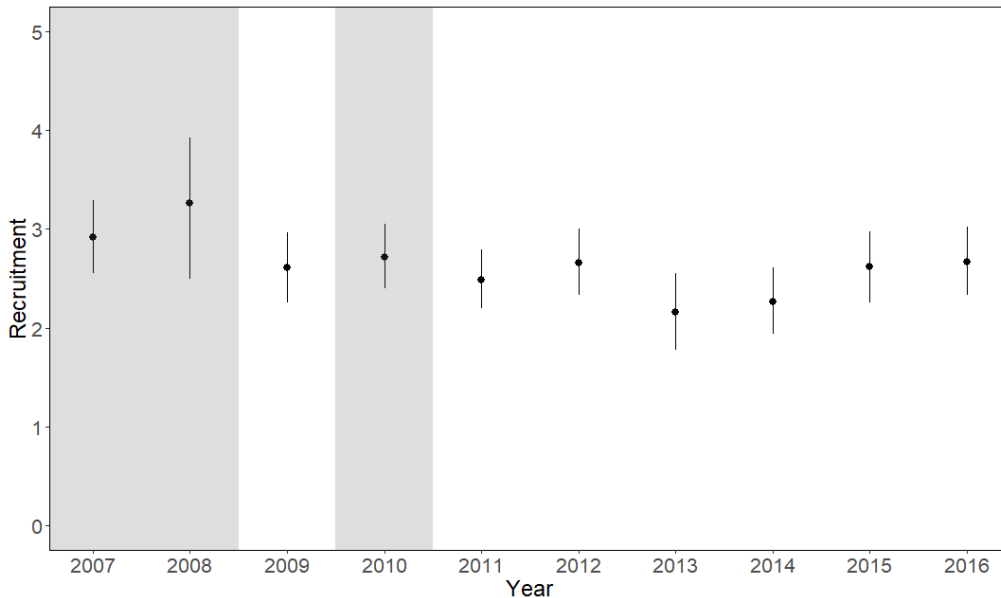


Figure 1.5. Estimates and 95% credible intervals of recruitment (mean pups per pack that survive 1 year) for wolves in Montana from 2007-2016. Shaded areas on the graph represent years without harvest.

Survival was greatest during years without harvest, and ranged from 0.70 (95% CI: 0.65-0.76) to 0.76 (95% CI: 0.70-0.82; Figure 1.4). During years with harvest survival ranged from 0.59 (95% CI: 0.55-0.64) to 0.68 (95% CI: 0.64-0.72). The estimated number of wolves increased slightly and became relatively stationary over time whereas the estimated mean pack size decreased. The mean number of pups recruited per pack was variable across years. Mean recruitment ranged from 2.16 (95% CI: 1.78-2.55) to 3.26 (95% CI: 2.55-3.92; Figure 1.5). Future work will include estimates of the total number of pups recruited to the population in addition to the mean recruitment rate per pack.

We found that the primary drivers of variation in recruitment was density dependence, pack size, and harvest. For every 10% increase in population size, per-pack recruitment is predicted to decrease by 1.3%. For each additional wolf per pack, recruitment is predicted to increase by 5%. Pack size was also the main factor driving breeding pair status of wolf packs in Montana (Mitchell et al. 2008). The credible interval for the effect of harvest on per-pack recruitment overlapped 0, but there was still a strong negative effect of harvest (88% probability). Years with harvest had an estimated 26% decline in recruitment. Mean recruitment in years without harvest was 3 pups per pack, and mean recruitment in years with harvest was 2.2 pups per pack. These estimates align closely with findings in Idaho (Ausband et al. 2015). Future work could evaluate a quantitative measure of hunting and trapping that would provide more information for setting harvest regulations.

Our estimates of recruitment, survival, and abundance were comparable to other studies for wolves. The number of pups recruited per pack varied little over time. Recruitment estimates for wolves in Idaho averaged 3.2 and 1.6 pups per pack to 15 months without harvest and with harvest, respectively (Ausband et al. 2015). Survival rate for wolves in the NRM prior to harvest implementation averaged 0.75 (Smith et al. 2010), which is comparable to estimates for wolves in Montana during years without harvest (mean=0.73). Similarly, survival rate for wolves in an unharvested population in Wisconsin was 0.76 (Stenglein et al. 2015). Survival rates for wolves in exploited populations in Yukon and Alaska averaged

0.56 and 0.59, respectively (Ballard et al. 1987; Hayes and Harestad 2000), which is similar to our estimates during years with harvest (mean=0.64).

1.6 Develop and Test Theoretical Models: Sub-Objective #3

Introduction

Variation in recruitment is a result of variation in at least one component of recruitment (i.e., probability a pack successfully reproduces, litter size, pup survival, and the number of breeding females per pack). Many factors could cause these components to vary such as human-caused mortality, prey availability, multiple litters per pack, disease outbreaks, and group size. We will develop theoretical models of recruitment to explore variation in components of recruitment because there are few data to estimate the contribution of those factors to overall pup recruitment.

The probability a pack successfully breeds could be influenced by survival of the breeding pair, time since pack establishment, food availability, wolf density, and pack size and composition (Fuller et al. 2003; Mech and Boitani 2003; Brainerd et al. 2008). Litter size could be influenced by food availability and age of the breeding female (Boertje and Stephenson 1992; Fuller et al. 2003). Pup survival could be affected by pack size and composition, conspecific density, food availability, human-caused mortality, disease, litter size, and whether or not there was more than 1 breeding female (Fuller et al. 2003; Almberg et al. 2009; Ausband et al. 2017*a; b*). The number of breeding females per pack could be influenced by pack size and conspecific density (Ausband 2018).

Understanding the factors that affect components of recruitment can help guide management actions. For example, if increased breeder mortality is reducing the probability a pack successfully breeds, and consequently recruitment, management could alter the timing of the season so it does not coincide with breeding. Conversely, if low food availability is decreasing pup survival different management actions might be taken.

Preliminary Methods

We will develop theoretical models to evaluate the effects of various factors on the components of recruitment. We will then estimate recruitment in packs as the product of the four components.

We will develop models based on hypotheses about how the above factors affect recruitment. These models will generate predictions of recruitment if the hypothesis is correct. Using data from Idaho (Ausband et al. 2015), we will compare predictions of recruitment from the model to observed recruitment data. Data include information on breeding pair status and fate, number of non-breeding adults, number of potential recruits and number recruited, and harvest for 16 packs from 2008 – 2016. The model(s) that most closely predicts recruitment will be most supported. The model with most support can then be used to estimate recruitment of wolves in Montana.

We will develop a baseline model, and predictions from the baseline model will serve as a comparison to predictions from other models. This baseline model will represent a null hypothesis that there are no factors that affect recruitment (i.e., mean rate with process variance).

Discussion

The empirical recruitment model provides more information about recruitment than the breeding pair estimator, but will require data to provide estimates. Although data requirements are less than current monitoring, a theoretical model may provide comparable accuracy and precision in estimates of recruitment with less data.

We are currently developing hypotheses about factors affecting the components of recruitment (probability a pack breeds, litter size, pup survival, and number of breeding females). We will begin running analyses in March 2019 to generate predictions of recruitment.

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OBJECTIVE 2: IMPROVE AND MAINTAIN CALIBRATION OF WOLF ABUNDANCE ESTIMATES GENERATED THROUGH POM—*Sarah Sells, Project 1*

2.1 Introduction

Monitoring is a critical yet challenging management tool for gray wolves. Monitoring results help MFWP set management objectives and communicate with stakeholders and the public. Monitoring any large carnivore is challenging due to their elusive nature and low densities (Boitani et al. 2012). This is particularly true for wolves in the Northern Rocky Mountains, as federal funding for monitoring has ended and a large population spreads monitoring efforts thin. Furthermore, there is frequent turnover of packs, and behavioral dynamics may have changed with harvest.

Abundance estimates are a key component of monitoring (Bradley et al. 2015). Abundance is currently estimated in Montana using 3 parameters: area occupied, average territory size, and annual average pack size (Fig. 2.1, Bradley et al. 2015). Area occupied is estimated with a Patch Occupancy Model (POM) based on hunter observations and field surveys (Miller et al. 2013, Rich et al. 2013, Bradley et al. 2015). Average territory size is assumed to be 600 km² with minimal overlap, based on past work (Rich et al. 2012). Annual average pack size is estimated from monitoring results. Abundance is then calculated as the number of territories estimated within the area occupied, multiplied by the average pack size.

Whereas estimates of area occupied from POM are expected to be reliable (Miller et al. 2013, Bradley et al. 2015), reliability of abundance estimates hinge on assumptions about territory size and overlap (Bradley et al. 2015). Assumptions of a fixed territory size with minimal overlap are simplistic; in reality, territories vary spatiotemporally (Uboni et al. 2015). This variability is likely even greater under harvest (Brainerd et al. 2008). Furthermore, estimates of mean territory size were largely derived pre-harvest (Rich et al. 2012). If average territory size has changed, abundance estimates would be biased. Similarly, at finer spatial scales (e.g., at regional levels), where territory sizes are smaller than average, abundance estimates would be biased low, whereas the opposite would be true where territories are larger than average. Variations in territory overlap would similarly bias results.

Estimates of abundance also hinge on assumptions about pack size (Bradley et al. 2015). Pack size estimates require packs to be located and accurately counted each year, which is no longer possible due to the large number of packs and declining funding for monitoring (Bradley et al. 2015). Since implementation of harvest in 2009, several factors have

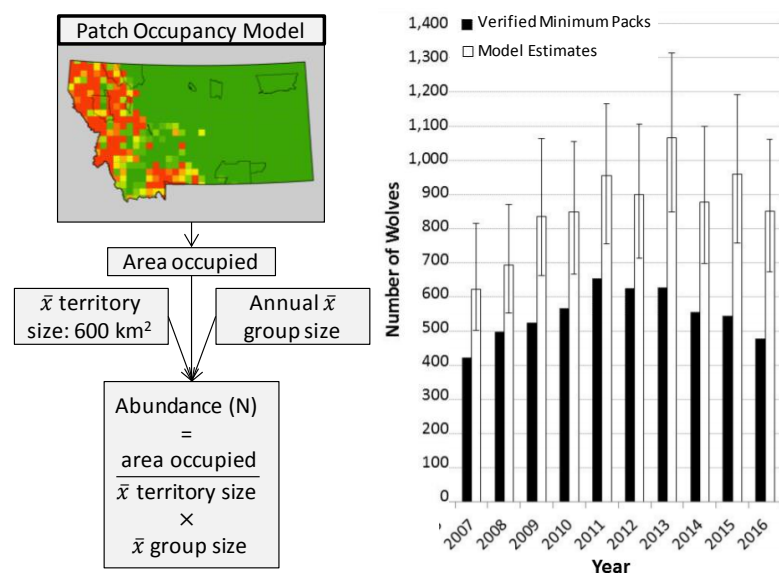


Figure 2.1. Example of POM results (red indicates highest occupancy probability, green lowest), and methods for calculating abundance. Graphed abundance estimates are based on minimum counts (black bars) and POM-based estimates (white bars). (Adapted from Bradley et al. 2015.)

further compounded these challenges and decreased accuracy of pack size estimates. First, whereas larger packs are generally easier to find and monitor, average pack size has decreased since harvest began (Bradley et al. 2015). Difficult-to-detect smaller packs may be more likely to be missed altogether, biasing estimates of average pack size high. Conversely, incomplete pack counts, especially for larger packs, could bias estimates of average pack size low. Harvest and depredation removals also affect social and dispersal behavior (Adams et al. 2008, Brainerd et al. 2008, Ausband 2015) and therefore further influence pack size.

Development of reliable methods to estimate territory size, territory overlap, and pack size could improve accuracy and precision of abundance estimates. In addition to pack counts, monitoring has relied on deploying collars; this is increasingly challenging and costly due to difficulty of capture and frequent collar loss caused by collar failures and mortalities (Table 2.1). Given these challenges, the fact that federal funding for wolf monitoring has ended, and the number of packs to be monitored, there is need for new methods that reduce monitoring requirements and enable estimating territory size, territory overlap, and pack size. Furthermore, these methods would ideally help keep estimates from POM calibrated into the future, which could be achieved by developing methods to predict behavioral changes under a wide range of potential future conditions.

Table 2.1. GPS collars deployed by MFWP on wolves (primarily in conjunction with this research) by year, and recorded numbers of collar failures and mortalities, as of February 2019. Collar failures include those missing (no fixes and no VHF signal), with outcome unknown. Cause of mortalities included harvest, poaching, depredation removals, vehicles, and conspecific aggression. Outcomes did not always occur the year of deployment, but nearly all failures and mortalities occurred < 2 years after deployment.

Year	Collars Deployed	Outcome		
		% Failed & MIA	% Mortality	% Other
2014	11	9.1	27.3	63.6 ¹
2015	14	28.6	57.1	14.3 ²
2016	29	51.7 ³	48.3	0.0
2017	18	38.9	50.0	11.1 ⁴
2018	20	10.0	50.0	40.0 ^{4/5}
Total	92	31.5	47.8	20.7

1. Collars were retrieved after dropping off as programmed.

2. Collars were swapped when wolf recaptured.

3. Includes 1 collar drop-off.

4. Collars remain functional and deployed.

5. Two additional collars appear to be in the process of malfunctioning (no recent fixes; 3 months w/o fixes demarcates failure).

2.2 Sub-Objectives of Objective #2

Improving and maintaining calibration of wolf abundance estimates generated through POM relies on multiple sub-objectives:

1. Develop theoretical and empirical models for territory size:

- Improve reliability of abundance estimates from POM.
- Eliminate the assumption that there is a single, fixed territory size statewide to enable predicting abundance at finer spatial scales (e.g., regional levels).
- Provide understanding of how territory size, overlap, and location will vary under potential future conditions (e.g., with increasing harvest or ungulate populations).
- Reduce the need for data (e.g., trapping, collaring, etc.) to keep POM calibrated into the future.

2. Develop theoretical and empirical models for group size:

- Improve reliability of estimates from POM.

- b. Eliminate the need for extensive monitoring of annual pack sizes.
 - c. Provide understanding of how group sizes will vary under future conditions.
- 3. Incorporate territory and group size models into POM:** provide MFWP with the tools for estimating abundance of wolf packs and individuals.

These sub-objectives will also contribute to the Study Objectives #3 & 4, developing an adaptive harvest management model and a recommended monitoring framework for MFWP.

2.3 General Approach

Our approach employs both theoretical and empirical models to evaluate the advantages, trade-offs, and appropriate applications of each. As theoretical and empirical approaches are complementary, using both will help maximize understanding of behavior. This in turn will provide models that can calibrate POM now and into the future while reducing the need for intensive monitoring efforts. A theoretical approach provides a means to test hypotheses about mechanisms driving behavior, such as why wolves select certain areas for their territories. If natural selection has sufficiently shaped mechanisms driving territorial or social behavior to be broadly consistent across space and time, a theoretical model based on these mechanisms can be useful across spatiotemporal extents. For example, harvest management may vary over time, as will ungulate populations. Through simulations, theoretical models can predict behavior across a full range of potential conditions that could be encountered now or in the future (Fig. 2.2). The empirical models will also reveal important patterns in territories and social behavior of wolves in Montana. The empirical models are likely to be reliable for the time and place they are developed (i.e., from recent monitoring and collaring efforts; Mitchell and Powell 2002). They can help evaluate the predictions and reliability of the theoretical models, and be applied alongside the theoretical models to calibrate POM. We will discern and provide recommendations on the appropriate applications for each.

We are developing and testing the models in multiple phases, starting with the territory model. Phase one (Sect. 2.4) is to develop a theoretical territory model and generate predictions of what should be observed empirically if our hypotheses for territory selection have support. Phase two (Sect. 2.5) is to develop empirical models to summarize patterns in territory sizes of wolves in Montana. Phase three (Sect. 2.6) is to compare the two approaches and produce final tools to calibrate POM.

Phase one of the territory model is complete, and phases two and three will soon be completed. We will repeat this three-phased approach for the group size models. The group size models will use the same techniques and much of the same data as the territory models. We have acquired the training and experience to code the theoretical models, and have collected and prepared the empirical data necessary for the group size models. Accordingly, development of the group size models will be greatly accelerated.

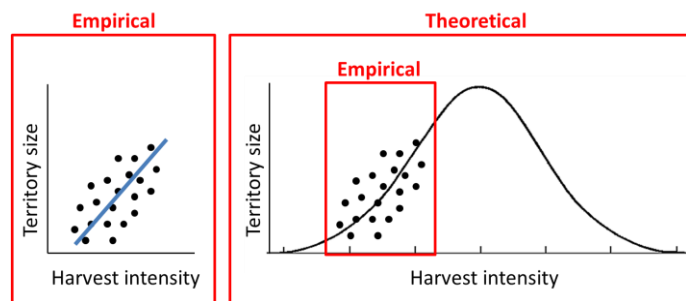


Figure 2.2. Inferences (e.g., about the effects of harvest on territory size) that might be drawn from an empirical study are reliable for the time and place from which empirical data were derived. A theoretical model can be used to simulate, test, and draw inferences from the full range of possibilities. Both approaches are complementary.

2.4 Territory Models: Phase One

Introduction

The goal of developing a theoretical territory model is to help calibrate POM by increasing understanding of how and why territories vary over space and time. This variation could arise based on the conditions wolves encounter when selecting and defending territories, such as those related to food resources, competition, and humans. Accordingly, understanding these effects could help estimate how and why territory size will vary in space and time. This information can in turn be used to calibrate POM. A theoretical model can generate predictions, based on the model's hypotheses, for what should be observed empirically if the model suitably captures the mechanisms driving territorial behavior. Suggesting potential utility of this approach, a similar approach was previously shown to be useful for understanding and predicting animal space use (Mitchell and Powell 2004, 2007, 2012).

Based on theoretical and empirical precedent, we hypothesized that wolves select territories economically to obtain sufficient resources for survival and reproduction, based primarily on the benefit of food resources (Brown 1964, Hixon 1980, Carpenter 1987, Adams 2001) and costs of competition (Brown 1964, Hixon 1980, Carpenter 1987) and travel (Mitchell & Powell 2004, 2007, 2012). This Base Hypothesis (H_B) provided predictions that should be observed empirically if our understanding of territory selection is correct.

Understanding how food resources might affect territorial behavior could help calibrate POM. Based on H_B , we hypothesized that if food resources are the primary benefit to territory selection, their heterogeneous distribution and abundance will affect territory selection. We thus simulated territory selection in landscapes with various distributions and abundances of food resources. This was important because a model for territory selection should be able to replicate observed relationships between food resources and territory size.

Understanding how intraspecific competition affects territorial behavior could also help calibrate POM. We hypothesized that if the cost of competition is inherent to territory selection, conspecific density will have important effects. We therefore simulated territory selection at a range of population densities to understand how competition could affect territory size and overlap.

Resource requirements could also have important effects on territory selection (e.g., if large or small packs have different resource requirements). We simulated territory selection for different levels of resources to understand how selection may differ if resource requirements vary. This also provided a means to evaluate robustness of predictions to varying resource requirements.

Understanding the effects of predation risk could help calibrate POM, because predation risk could drive territory selection for some populations (Sargeant et al. 1987, Whittington et al. 2005, Rich et al. 2012). Accordingly, we developed a variation of H_B to include the cost of predation risk (H_P). Predation risk for wolves is primarily associated with humans; therefore, the risk of harvest by humans could affect territory selection. Similarly, this cost may not be a driver in areas of limited or no harvest, such as in Yellowstone National Park (YNP).

Methods

We developed a mechanistic, spatially-explicit individual-based model (IBM) for territory selection in the program NetLogo 6.0 (Wilensky 1999). We simulated landscapes to represent a range of conditions that could be encountered by wolves, and simulated territory selection by instructing simulated wolves (agents) to select territories.

Landscapes

We represented each landscape as a continuous grid of 200×200 patches (Fig. 2.3). Each patch varied by its food resources (B) and predation risk (P).

Landscapes varied in overall:

1. Food distribution: the spatial distribution of patches with high B (evenly distributed, moderately clumped, or highly clumped).
2. Food abundance: landscape-wide ΣB (low, medium, or high, and = across food distributions).
3. Predator abundance: landscape-wide ΣP (low, medium, or high).

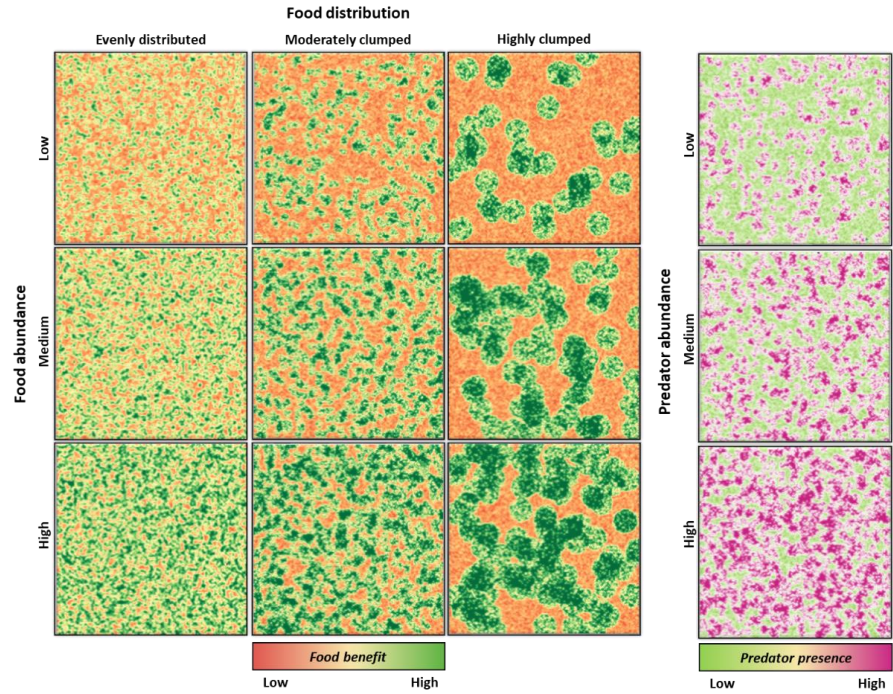


Figure 2.3. In phase one of the theoretical territory model, each simulated landscape was a grid of 200×200 patches. Each patch varied in its benefit of food (B) and presence of predators (P). Entire landscapes varied in overall distribution and abundance of food and abundance of predators, i.e., in the spatial distribution and sum of B and distribution of P . No 2 landscapes were identical.

Agents

Agents represented different packs. In any given simulation, agents were assigned a threshold of resources they required for survival and reproduction (low, medium, or high).

Territory selection

For each simulation, the model cycled through a series of processes (Fig. 2.4) through which territories and competition among agents emerged on the landscape (e.g., Fig. 2.5). Agents were added to the landscape one by one, representing dispersal of an agent in search of a territory. A territory was established for the agent by identifying patches of high value, based on selection algorithms representing hypotheses H_B and H_P (Appendix A). If an agent's territory overlapped another or patches formerly shared were later abandoned, territories for affected agents were shifted if economical to do so. Effects of competition were thus dynamic (i.e., changed throughout the simulation) and density dependent.

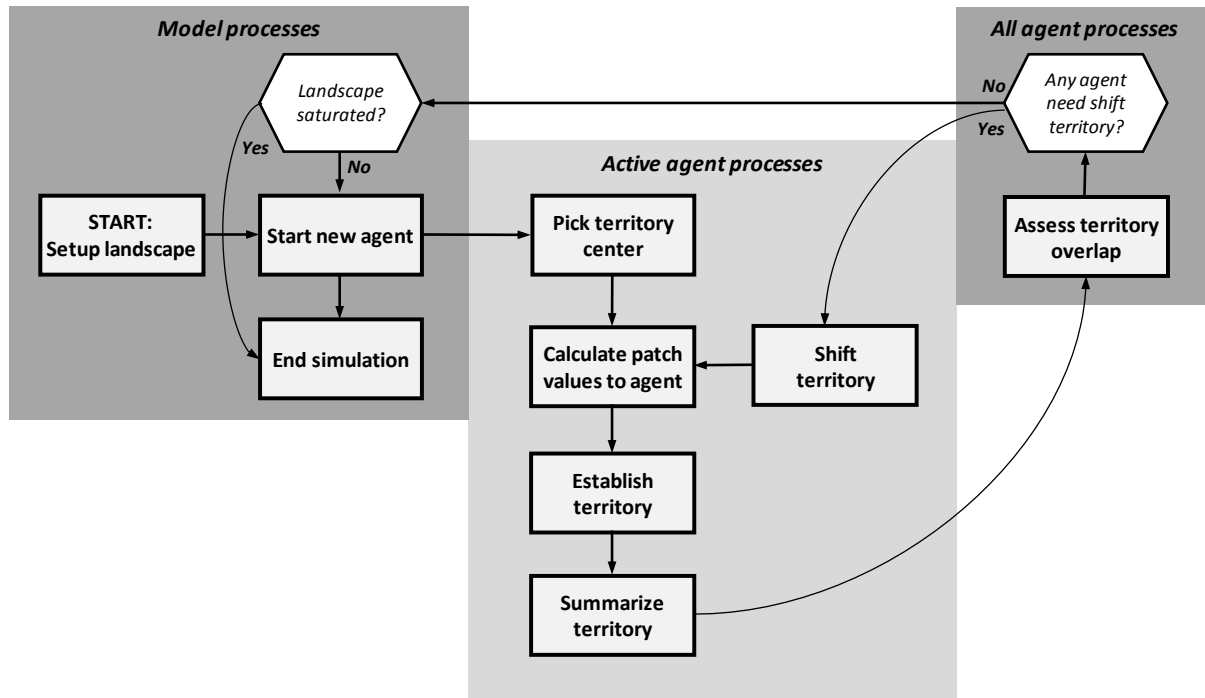


Figure 2.4. The theoretical territory model employed a cycle of processes (Appendix A). After the landscape was created, an agent was added. A territory was established for the agent by identifying patches of high value. The number of territories gradually increased as more agents were added to the landscape. If an agent's territory overlapped another or patches formerly shared were later abandoned, territories for affected agents were shifted if economical to do so. Effects of competition were thus dynamic (i.e., changed throughout the simulation) and density dependent.

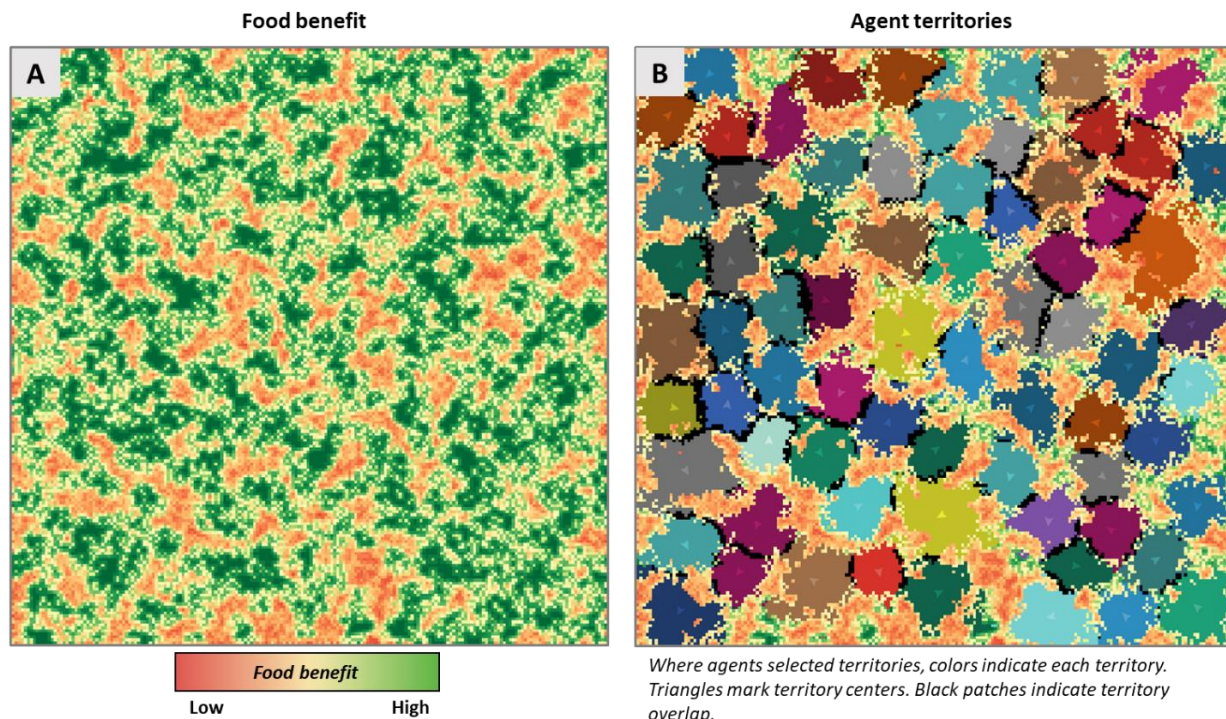


Figure 2.5. As an example of a simulated landscape where agents formed territories in the theoretical territory model, Panel A shows the food-benefit of patches; Panel B shows 71 resulting territories (mean size of 371 patches, range 266 – 670).

Analyses

Throughout the simulation, for each agent we measured territory size (# of patches), overlap (proportion of the territory shared with >1 agent), and competitor pressure (# of territories present at territory establishment). At the end of each simulation, we measured the landscape's territory abundance (representing a saturated population) and each agent's final territory size and overlap.

We summarized results with program R (R Core Team 2018). We calculated mean territory size and overlap across independent variables (e.g., food distribution, food abundance, predator abundance, etc.) for low density and saturated populations. We summarized the initial and final territory size and overlap in relation to competitor pressure.

Results and Discussion

Agents formed >174,000 simulated territories in total, the summaries of which provide predictions for what should be observed empirically if our hypotheses have support. For brevity here, we report the primary patterns predicted by the model. Full detail will be presented in an upcoming manuscript.

Effects of food resources

Food resources are predicted to strongly affect territory size and overlap, demonstrating how differences in prey populations could affect the size and overlap of wolf territories in Montana. This in turn could have important implications for POM. More clumped or abundant food resources are predicted to result in smaller territories (Fig. 2.6). Fluctuating prey populations could thus

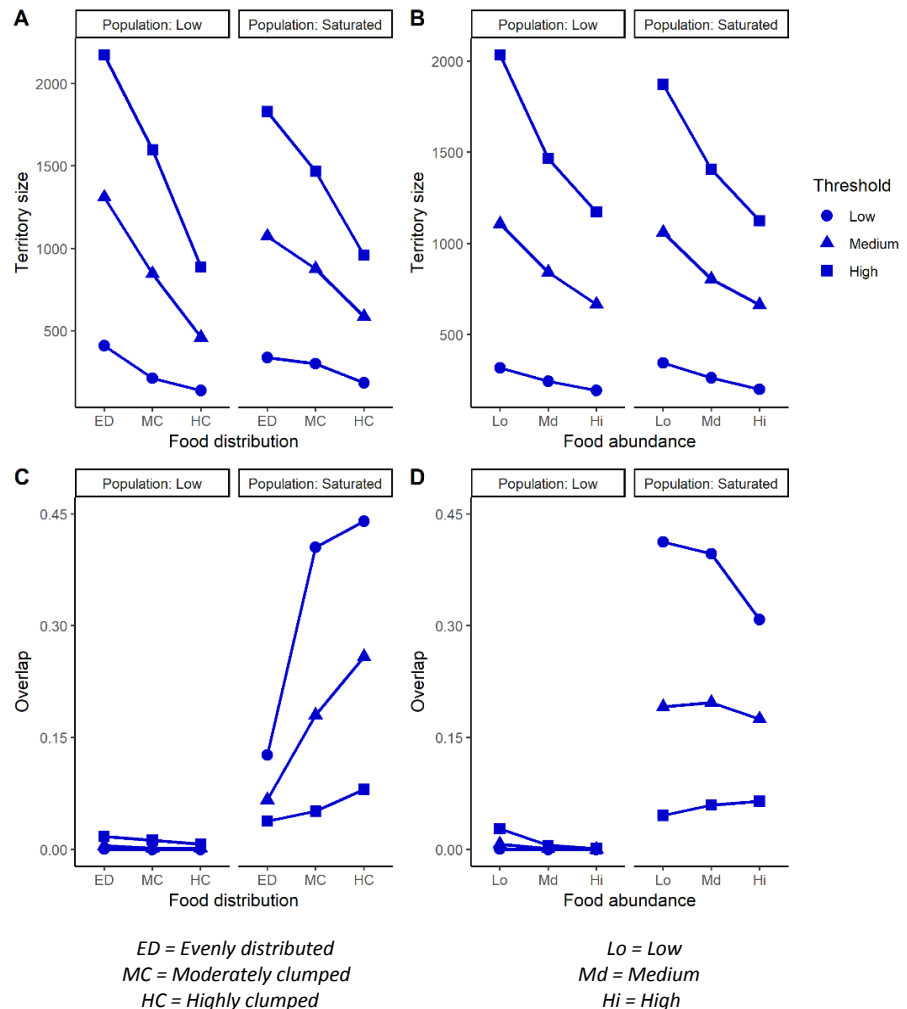


Figure 2.6. Results from phase one of the theoretical territory model. Territory size (# of patches) and overlap (proportion of the territory belonging to >1 agent) varied in response to food distribution (left panels), food abundance (right panels), population density (columns), and resource threshold (shapes).

cause territory size to also fluctuate, which could affect accuracy of yearly abundance estimates from POM. At high population densities (i.e., likely for many packs in Montana today), overlap is predicted to be greater where food resources are more clumped, and to vary less across food abundances. Additionally, territory sizes and overlap are predicted to vary widely among packs, particularly under certain prey distributions and abundances (Fig. 2.7). Carrying capacity is also predicted to be higher where food resources are more clumped or abundant (Fig. 2.8). These predictions indicate that the density of territories may be greatest in areas of Montana with high prey abundance arranged in more clumped distributions. Territories in these areas, however, may also demonstrate the largest variation in size.

Emergence and effects of competition

Competition among packs is predicted to strongly affect territory size and overlap, which could affect accuracy of abundance estimates from POM. Competition is predicted to affect the variation in territories among packs. For each new territory formed, its size and overlap at establishment are predicted to be on average greater than that of its predecessors (Fig. 2.7). This pattern in territory size is predicted to remain consistent as population density increases, and suggests that the newest territories formed in Montana may be among the larger observed. As an exception, however, where food is evenly distributed, new territories are predicted to be smaller at establishment than those of predecessors.

Overlap is also predicted to vary across packs (Fig. 2.7). In high-density populations, territories that were established either relatively earlier or later in time are predicted to have the most overlap, whereas those

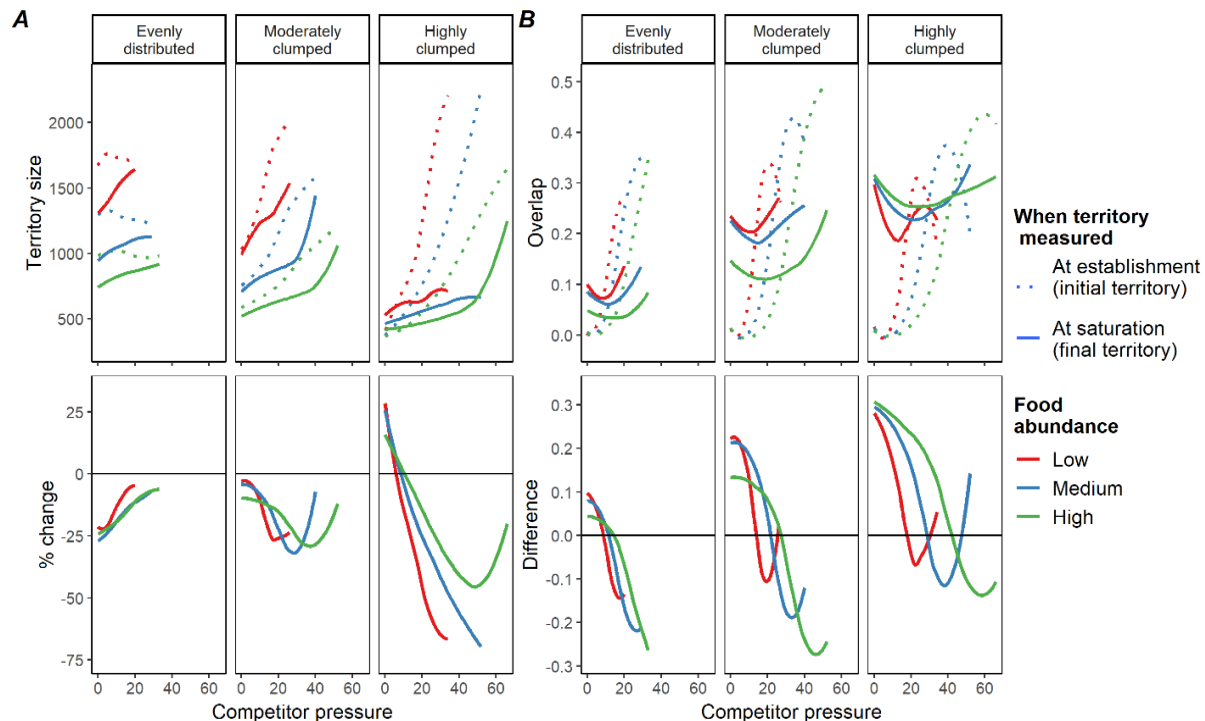


Figure 2.7. Results from phase one of the theoretical territory model. Competitor pressure (the number of agents at the time of territory establishment) affected territory size (# of patches) and overlap (proportion of the territory belonging to >1 agent). Effects varied by food distribution (panels) and abundance (colors). In A, lower panels (% change) depict the change in territory size as competition increased, i.e., from the initial territory selected at time of establishment to the final territory at the end of the simulation. In B, lower panels (Difference) similarly depict the difference in proportion of overlap as competition increased. Smoothed conditional means are shown for agents with medium resource thresholds; results for other thresholds were similar.

established at a medium population density are predicted to have the least. This suggests that density of territories may increase most noticeably in areas colonized the earliest during wolf recovery in Montana.

Competition is also predicted to affect each pack's territory over time (Fig. 2.7). This could have implications for abundance estimates in POM, as continual competition for space could affect territory size and overlap year-to-year. After establishing a territory, a pack's territory size is generally predicted to decrease over time as competition increases. Where food resources are highly clumped, however, territory size is predicted to expand for a portion of packs. Whether a pack's overlap with other territories increases or decreases is predicted to depend on the population density encountered at territory establishment. Packs that established territories at lower densities are predicted to have an increase in overlap over time, whereas the opposite is predicted for packs that established more recently.

The predicted interactions between competition and food resources (Fig. 2.7) suggest the importance of accounting for both considerations when estimating territory size and overlap to calibrate POM. Additionally, it appears that the means by which competition is measured can affect inference (Fig. 2.9). Territory size is predicted to have an overall positive relationship with the number of competitors near a pack's territory border. After scaling the number of competitors by territory size, however, this relationship is predicted to be negative.

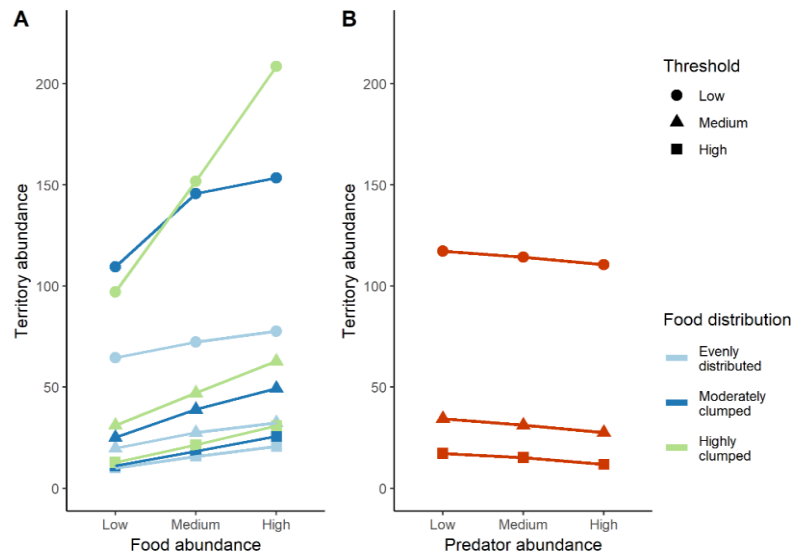


Figure 2.8. Results from phase one of the theoretical territory model. Territory abundance at saturated population densities was affected by food distribution and abundance (Panel A) and predator abundance (Panel B).

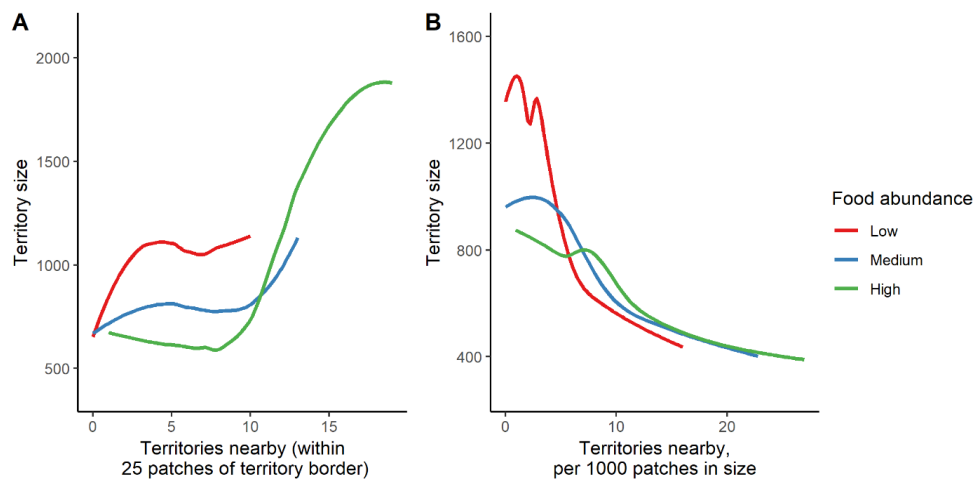


Figure 2.9. Results from phase one of the theoretical territory model. The relationship between territory size (# of patches) and the # of nearby competitors (those within a 25 patch radius of the territory border) varied depending on how this measure of competition was assessed (as a raw number, Panel A; or accounting for size of the territory, Panel B). Smoothed conditional means for a medium resource threshold are shown.

Effects of threshold

If packs have sufficiently large differences in resources required for survival and reproduction, this could affect their territory size and overlap, which in turn could affect abundance estimates from POM. Packs with higher resource requirements are predicted to have larger territories with less overlap (Fig. 2.6). Logically, carrying capacity and resource requirements are predicted to be inversely related (Fig. 2.8). Effects of resource requirements are also predicted to interact with food distribution and abundance. For example, whether overlap is positively or negatively correlated with food abundance is predicted to depend on resource requirements (Fig. 2.6).

Effects of predation risk

Territories are predicted to vary with predator abundance (Fig. 2.10). This could affect abundance estimates from POM. If wolves experience varying levels of harvest pressure as changes in predator abundance, harvest pressure could produce variable effects depending on the food resources and competition wolves encounter in an area. The most noticeable effect, however, may be in overlap rather than in territory size. Where predator abundance is higher, overlap is predicted to be lower, especially where food resources are more clumped. In contrast, territory size is predicted to have either a slightly negative correlation with predator abundances or no relationship, depending on the population density, food distribution, and food abundance on the landscape. Carrying capacity is also predicted to be slightly lower where predator abundance is greater (Fig. 2.8), which suggests the state may be able to support fewer packs during eras of harvest management.

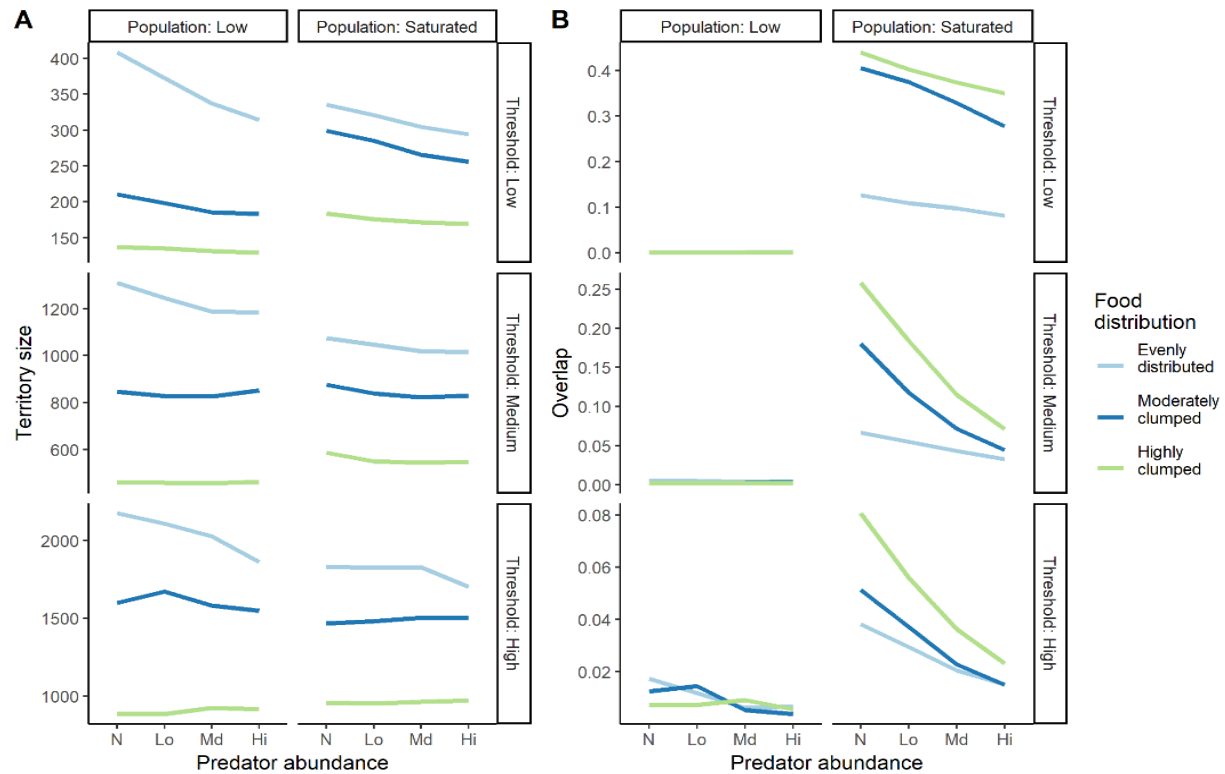


Figure 2.10. Results from phase one of the theoretical territory model. Agents encountered a predator abundance of low – high on any given landscape. Results show territory size (# of patches) and overlap (the proportion of the territory belonging to >1 agent) often varied in response to predator abundance, but territory overlap varied more strongly than did territory size. (Abundance of N = none, i.e., agents ignoring the cost of predation risk under H_B .)

Preliminary tests of predictions

Additional phases of this work involve testing the model's predictions for wolves in Montana; however, we also conducted a literature search at the end of phase one to evaluate preliminary support for the model. The model's hypotheses could apply to many species, so we reviewed the literature for any papers discussing patterns in territory size and overlap. We found that predictions from the model have been observed empirically in many taxa (Table 2.2). Additional tests of the theoretical territory model will occur in phases 2 and 3.

Table 2.2. Predictions from phase one of developing the theoretical territory model, and evidence of support we identified in the literature, after developing the model. Because our hypotheses would be the same for many species, the predictions can be tested across taxa to determine support for the hypotheses.

Prediction	Observed empirically?	Citations
<i>Mean territory size ↓ w/ ↑ food clumping (Fig. 2.6)</i>	Yes, in badgers (<i>Meles meles</i>) and dingos (<i>Canis lupus dingo</i>).	Kruuk and Parish 1982, Newsome et al. 2013
<i>Mean territory size ↓ w/ ↑ food abundance (Fig. 2.6)</i>	Yes, in numerous species including mollusks, fish, lizards, birds, and mammals. Territory size was also reported to increase with latitude, where productivity is generally lower.	Stimson 1973, Slaney and Northcote 1974, Simon 1975, Hixon 1980, Smith and Shugart 1987, Gompper and Gittleman 1991, Adams 2001, Mech and Boitani 2003, Jedrzejewski et al. 2007, Gillman et al. 2015, Kittle et al. 2015
<i>Mean territory overlap ↑ w/ ↑ food clumping (Fig. 2.6)</i>	Yes, in dunnocks (<i>Prunella modularis</i>).	Davies and Hartley 1996
<i>Mean territory overlap ↑ or ↓ w/ ↑ food abundance (Fig. 2.6)</i>	Unknown. ¹	
<i>Mean territory size ↑ w/ ↑ competitors (Figs. 2.6-2.7)</i>	Inconclusive. ² Territory size in song sparrows (<i>Melospiza melodia</i>) was positively correlated with the number of competitor species, which researchers attributed to increased competition. In various species, population-level mean territory size was often reported to decrease rather than increase. Our predictions that territories often noticeably compress with increasing competitor pressure appear to align with these empirical observations and others showing that intruder pressure was negatively correlated with territory size.	Yeaton and Cody 1974, Myers et al. 1979, Ewald et al. 1980, Stamps 1990
<i>Mean territory overlap ↑ with competition (Figs. 2.6-2.7)</i>	Yes, overlap increased at higher densities in various species.	Reviewed by Stamps 1990
<i>Individual territory size ↑ for later colonizers than earlier</i>	Unknown. ¹	

colonizers (Fig. 2.7)

<i>Individual territory size generally compressed as competition continues to ↑ (Fig. 2.7)</i>	Yes, intruder pressure was negatively correlated with territory size in various species.	Myers et al. 1979, Ewald et al. 1980, Stamps 1990
<i>Individual territory overlap ↑ or ↓ w/ ↑ competitors (Fig. 2.7)</i>	Inconclusive ¹ , insufficient details in literature.	
<i>Territory abundance ↑ w/ ↑ food abundance (Fig. 2.8)</i>	Yes, predator biomass and abundance was shown to positively correlate with prey biomass.	Stimson 1973, Slaney and Northcote 1974, Carbone and Gittleman 2002
<i>Territory size ↓ w/ ↑ # nearby competitors, after scaling by territory size (Fig. 2.9)</i>	Yes, wolf territory size decreased with each additional nearby pack after scaling by territory size.	Rich et al. 2012
<i>Territory overlap ↓ w/ ↑ predator abundance (Fig. 2.10)</i>	Unknown. ¹	

1. Patterns appeared to be less commonly reported in the literature; none were found for these predictions.

2. Inconclusive support for these predictions could be due to insufficient data. We measured territory size including overlap, and its exclusion could generate the impression that population-level mean territory size decreases with increased density. Our predictions could also be correct yet difficult to fully detect empirically given the challenges of measuring what an animal selects and defends as its territory. If a low population density leads to fewer constraints and lower costs of competition, territories may appear large and nebulous in part as a result of exploratory movements, i.e., those beyond the defended territory. We measured territory size excluding exploratory movements, whereas it is difficult to know empirically what movements are exploratory.

2.5 Territory Models: Phase 2

Introduction

Phase two of territory model is ongoing and involves developing a set of empirical territory models that summarize patterns in territory sizes of wolves in Montana. This will provide the opportunity to produce models to compare and contrast with the theoretical model. The empirical territory models will also enable testing the predictions from the theoretical model. Additionally, this phase provides an opportunity to build on past work. Rich et al. (2012) investigated patterns in territory size during years with limited or no harvest. If territorial behavior has changed under harvest, new empirical models will enable identifying these effects.

Methods

We are currently developing the empirical territory models. Efforts have focused on preparing wolf location data, estimating territory size and extent, preparing data for independent variables, and conducting univariate analyses.

Preparing wolf location data

Since 2014, MFWP has deployed GPS collars in packs across western Montana. Collar types were Telonics store-on-board collars (TGW-4400-3), Telonics Iridium collars (TGW-4483-3 and TGW-4577-4), Lotek LifeCycle collars, and Lotek Iridium collars (Litetrack B 420). Collars were programmed to collect latitude and longitude every 3 – 13 hours for 2 – 5 years. Actual fix rates and collar life varied due to technological difficulties. We also gathered and used any preexisting datasets from GPS-collared wolves in Montana, including those from Rich et al. (2012) and as part of other research by MFWP.

Collar deployment was conducted by MFWP using ground or aerial capture. Ground capture was conducted with foothold traps designed to reduce injury (EZ Grip # 7 double long spring traps, Livestock Protection Company, Alpine TX). Aerial capture was conducted by MFWP-contracted crews using helicopters and dart guns. Wolves were anesthetized and handled in accordance with MFWP's biomedical protocol for free-ranging wolves (Montana Fish, Wildlife and Parks 2005) and guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

We prepared wolf location data for analysis by defining whether each wolf was a resident or disperser at any given time. Separating these two statuses avoided over-estimating territory size, as dispersal indicated a wolf's decision to change its territory. We mapped each wolf's fixes and noted clusters of fixes. These clusters appeared as localized movements and were generally easily detectable. We defined dispersal as the wolf's departure from the current cluster of fixes. Some dispersals were easily detectable, as the wolf left the cluster of its original territory in an outward trajectory and did not return. Alternatively, some wolves began making apparent forays, i.e., trajectories looping out of and back into the original cluster of fixes. These forays were often short-term (days or weeks), and tended to occur multiple times before the wolf either did not return, or made fewer or no new foray trips. If the wolf continued making at least one foray out of the cluster with <1 month between forays, we defined the wolf as a disperser beginning on the date of the first foray. If >1 month lapsed between forays, the wolf kept its status as a resident.

Dispersing wolves were either successful (i.e., a new cluster of fixes indicated they had joined an existing pack or set up a new territory), or were killed while dispersing (e.g., by wolves, hunters, vehicle strikes, etc.). Once a disperser's movements localized to a new cluster of fixes, we defined it as a resident. In rare cases, a wolf failed to generate an obvious cluster of fixes and appeared to possibly be nomadic, acting as a floater across and near many other known territory centroids. Also in rare instances, a resident wolf made sufficiently large forays to potentially greatly inflate their territory estimates, overlapping multiple other territory centroids. We noted our uncertainty in defining the territory boundaries for these wolves to enable running analyses with and without their data.

Estimating territory sizes

After preparing the wolf location data, we estimated territory sizes and locations using 95% volume-adaptive kernel density estimates (KDEs; Worton 1989). To do so, we used Program R (R Core Team 2018) with package AdehabitatHR (Calenge 2006), and set the smoothing parameter at 100% of the reference bandwidth. These methods slightly differ from Rich et al. (2012) who used a 90% kernel with 80% of the reference bandwidth. Our methods appeared to produce reasonable estimates that avoided generating lacunas or disjoint areas without appearing to appreciably inflate the territory boundary.

We estimated a KDE for the first year of data for each territory in which the wolf was a resident. We repeated these estimates for the second year of data where available. (A wolf that dispersed could have ≥ 2 territories, and a wolf remaining >1 year could have multiple estimates of the same territory.) We considered each estimate to be a reliable estimation of an annual territory if fixes spanned $\geq 70\%$ of a year. We censored wolves that emigrated out of Montana. Where an annual territory was represented >1 year by a reliable estimate, we averaged results. We will repeat these steps to estimate seasonal territory sizes (i.e., winter, October 15 – April 14, and summer, April 15 – October 14) to also evaluate patterns in seasonal territories.

We will update the GPS collar dataset before finalizing phase two. 10 collars remain deployed and functional, and 27 likely remain deployed but have malfunctioned. The functional collars should continue providing data in 2019, and the malfunctioning collars will provide additional data if found (i.e., via harvest or other mortality).

Preparing data for independent variables

Following Rich et al. (2012) and to test predictions from our theoretical models, our goal was to generate explanatory variables to represent prey resources, competition among neighboring packs, costs of travel, and risk of harvest by humans. Accordingly, the hypotheses in Section 2.4 also apply here. We completed the following steps in Program R (R Core Team 2018).

To represent prey resources, we generated statewide spatial density indices for deer (*Odocoileus virginianus* and *O. hemionus*) and elk (*Cervus canadensis*). Because data were not available by deer species for some of the following steps, we created a single density index for deer. Contrasting Rich et al. (2012), we did not use CPUE alone to represent deer and elk abundance because CPUE is influenced by and does not account for social considerations, terrain, or cover (K. Proffitt and K. Podrutzny, pers. comm.). Our indices make use of readily-available data and appear to reduce some of the issues of using CPUE alone. To create the indices, we delineated each species' seasonal distribution by converting into raster format datasets of predicted suitable habitat for winter and summer (Montana Natural Heritage Program). We identified the most recent 10-year average estimates of each species' abundance by MFWP region (fwp.mt.gov). We then calculated the area of each seasonal habitat in each region, and created a preliminary density index (*PDI*) by dividing the regional estimates of abundance by their estimated area of seasonal habitat. We assigned each raster cell its *PDI*. We then calculated the mean catch per unit effort (CPUE) from 2004 – 2017 for each hunting district (HD) by dividing the total harvest by hunter days, based on harvest estimates (<https://myfwp.mt.gov/fwpPub/harvestReports>). We assigned CPUE to each raster cell (*CPUE_{at cell}*) delineated as seasonal habitat within the HD. We calculated the mean CPUE by region (*CPUE_{regional mean}*). We calculated a revised density index as:

$$\text{Density index} = \text{CPUE}_{\text{at cell}} \div \text{CPUE}_{\text{regional mean}} \times \text{PDI}$$

This slightly bolstered or reduced the index in HDs with higher or lower CPUE, which is assumed to be associated with abundance (Rich et al. 2012). We interpolated this index into parks and reservations (for which data were not available) through inverse distance weighting. We smoothed the index (reducing the effects of large changes across HD boundaries) by calculating a weighted moving window value of the cell's nearest neighbors (a 5×5 km area). Finally, we measured the average of the summer and winter prey indices within each KDE.

We calculated competition as the number of packs near each territory. We buffered each territory by 25 km, and overlaid this area with the estimated centroids of nearby packs. Centroid data were prepared each year by MFWP, Idaho Fish and Game, and YNP (this larger extent was needed for packs near Montana's border). We identified the number of neighboring centroids intersecting the wolf's buffered territory, and used this value as an index to competition. As a second measure of competition controlling for territory size, we divided each KDE's count of neighboring packs by its territory size and multiplied this value by 1000 (Rich et al. 2012). This provided a means to estimate the change in territory size for each additional pack per 1000 km² in territory size.

We hypothesized that ruggedness affects travel costs for wolves. We modeled terrain ruggedness per km² as the Vector Ruggedness Measure (Sappington et al. 2007) using R package *spatialEco* (Evans 2018) and elevation data derived through package *elevatr* (Hollister and Shah 2017). We calculated the mean ruggedness within each KDE.

We are currently developing datasets to represent risk of harvest by humans. We hypothesized that cover type influences risk of harvest, and classified each km² as forested, open (e.g., sagebrush, grasslands, or barren areas), or human-dominated (e.g., cities or agricultural areas) based on existing vegetation type (LANDFIRE 2014). Because we hypothesized that roads may increase exposure to humans, we calculated the mean road density per km² using the most recent TIGER road dataset (U.S. Census Bureau 2018). (We also hypothesized that low-use roads may decrease travel costs and therefore territory size.) We hypothesized that greater human density would correspond with risk of harvest, so estimated human density per km² (U.S. Census Bureau). We also hypothesized that public lands would increase the risk of harvest by humans by providing greater hunter access than most private lands, so we classified each km² as public or private land. We will also prepare datasets for regional wolf hunting and trapping success rates, or additional datasets to represent risk of harvest by humans. We are calculating the average values of these indices within each KDE.

Analyses

Analyses are ongoing. We are using generalized linear models (GLMs) to identify patterns in territory size, similar to Rich et al. (2012). We are first running univariate analyses, the results of which we will use in phase three to evaluate support for predictions generated in phase one. We are considering $p \leq 0.05$ and omission of 0 from confidence intervals as indicative of strong support, and $p \leq 0.10$ as indicative of potential support. After identifying correlation among covariates, we will build competing multivariate models that avoid pairing overly-correlated covariates in any single model. We will identify the most predictive multivariate model using Akaike's information criterion (Burnham and Anderson 2002).

Preliminary Results and Discussion

GPS collar data and estimated territory sizes

From January 2014 – January 2019, 95 wolves were captured and collared with GPS collars in conjunction with this research. 14 wolves were GPS-collared from 2008 – 2009 in conjunction with Rich et al. (2012)'s work. An additional wolf was GPS-collared in 2012 as part of other research in MFWP.

We identified 144 annual territories whose boundaries were at least partially within Montana. Excluding territories with fixes spanning <70% of the year yielded 52 annual territories. Each remaining territory had 69 – 4278 fixes ($\bar{x} = 903.02$, $SE = 125.67$). After averaging results for individuals with >1 year in the same territory, there were 45 unique territories. Of these territories, we identified 2 wolves as having uncertain territory boundaries due to large forays that were unlike behavior of other wolves in our dataset. We censored these 2 wolves from univariate analyses.

Mean annual territory size of all 45 territories was 649.86 km² ($SE = 73.76$ km², range 187.71 – 2479.91 km²). After censoring the 2 wolves with uncertain boundaries, mean size was 579.75 km² (Fig. 2.11; $SE = 56.71$ km², range 187.71 – 2207.42 km²). Estimates did not vary as a function of number of fixes ($p = 0.936$).

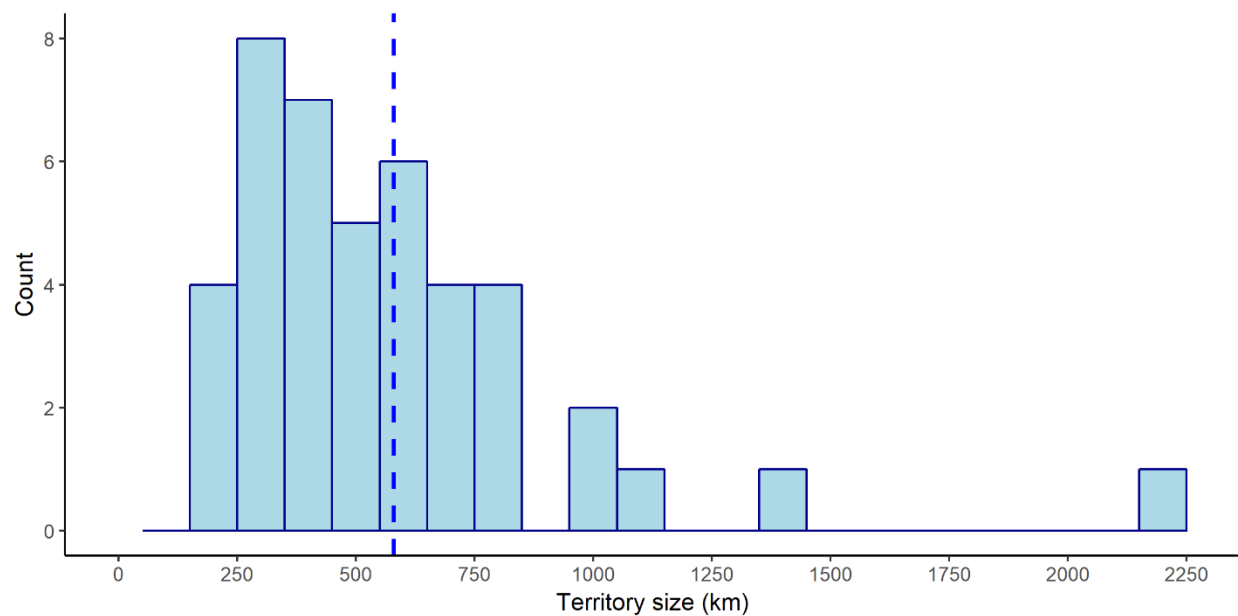


Figure 2.11. Estimated territory sizes (km²) of 43 GPS-collared wolves in Montana, 2008 – 2018 (after censoring 2 wolves with uncertain boundaries). The blue dashed line demarcates the mean territory size (579.75 km²). Results will be used in phases two and three of developing the territory models.

Preliminary univariate analyses

Territory size had a negative relationship with several measures of prey abundance. This supports our hypothesis that food resources will affect territory size. For every 1-unit increase in the deer summer density index, annual territory size decreased by 16.17% (95% $CI = -1.596 - 30.833$, $p = 0.080$; 90% $CI = 1.496 - 28.662$). Similarly, each 1-unit increase in the deer winter density index led to an 8.30% decline in territory size ($CI = 1.428 - 14.695$, $p = 0.024$). Combining the indices for deer and elk, each 1-unit increase in the summer or winter density index led to a decline in territory size of 19.88% ($CI = 0.849 - 35.271$, $p = 0.048$) and 9.73% ($CI = 4.266 - 14.891$, $p = 0.001$), respectively. Territory size did not vary in relation to the elk indices alone ($p > 0.10$).

Territory size had a positive or negative relationship with competition, depending on how competition was measured. This supports our hypothesis that competition will affect territory size. For every additional pack centroid ≤ 25 km of a wolf's territory boundary, territory size increased by 12.48% ($CI = 6.618 - 18.665\%$, $p = <0.001$). Territory size decreased by 5.01% ($CI = 3.099 - 6.891\%$, $p = <0.001$), however, for each additional nearby centroid per 1000 km² in territory size. We also noted that territories compressed in 8 out of the 11 instances that territory estimates were available across multiple years.

Univariate analyses did not reveal evidence of a relationship between territory size and ruggedness, cover type, human population density, or land ownership ($p > 0.10$). Territory size decreased by 22.80% for every additional road per km² ($CI = -1.154 - 41.080$, $p = 0.067$; 90% $CI = 3.147 - 38.464$). This could support our hypothesis that roads decrease travel costs; as a next step, we will differentiate roads as high- or low-use to further evaluate these results. Additional work is ongoing to finalize a layer to represent the cost of predation risk for wolves.

2.6 Territory Models: Phase 3

Introduction

Phase three of the territory models is ongoing and provides the final development, analysis, and comparison of the theoretical and empirical models. This will enable us to prepare final tools that can be used to calibrate POM, and recommendations for when each application may be most appropriate.

Methods

Phase three involves multiple steps, the first of which is a comparison of the predictions from phase one with the empirical results from phase two. This will enable discerning the theoretical model's predictive power and potential weaknesses.

To further evaluate the theoretical model, we will use it to predict size and overlap of wolf territories in Montana by adding data to the simulations. Using the data we prepared in phase two (i.e., deer and elk indices, terrain ruggedness, and human influence), we will re-create the landscape to represent Montana. We will run new simulations to predict size, overlap, and variation in wolf territories across Montana (e.g., measuring territory size in km² rather than # of patches). We will summarize results in figures similar to those from phase one and further compare the theoretical model's predictions to the results from phase two. We will also identify the theoretical model's capacity for producing spatially-explicit predictions. To do so, we will compare predicted locations of territories to those estimated for GPS-collared wolves (Section 2.5) and locations of cells estimated by POM as occupied. Although the ability to make spatially-explicit estimates of territory locations is not necessary for calibrating POM, this could also be useful and increase our understanding of wolf behavior and abundance.

The final steps of phase three will be a formal comparison of the theoretical and empirical models, and recommendations for their use in POM. We will use each to predict territory sizes in Montana, and contrast their results to identify areas of agreement, disagreement, and uncertainty. We will then provide demonstrations and advice for when and how to use each in POM.

Preliminary Results and Discussion

Univariate analyses from phase two (Sect. 2.5) appear to support the theoretical model's predictions from phase one (Sect. 2.4). As predicted (Fig. 2.6), greater food abundance was associated with significantly smaller territory sizes for wolves in Montana. Territory size did not vary in relation to the elk indices alone. This could indicate more work is needed in developing these indices, or the elk indices simply are not predictive on their own; multivariate analyses will reveal if this is true. As predicted by the theoretical model (Fig. 2.7 & 2.9), territory size of wolves in Montana had either a positive or negative relationship with competition, depending on how competition was measured. Additionally, the theoretical model predicted predator abundance would not strongly affect territory size (Fig. 2.10); we found no significant relationship between territory size and our measures for predator abundance.

In preparation for its final simulations, we have prepared and added data from phase two to the theoretical model. Preliminary simulations demonstrate that the model predicts territories will occur in approximately the same areas in Montana as occupied by existing packs (Fig. 2.12). Final simulations will begin shortly, after which we will summarize final results. These will provide estimates for how territory size and overlap will vary under a wide array of circumstances.

No further simulations with the theoretical model will be necessary after completion of phase three. For example, results will estimate territory size and overlap in specific areas of the state based on relative levels of harvest and characteristics of local ungulate populations (e.g., Fig. 2.13). We will produce estimates from the empirical model, as well. These estimates could be made spatially explicit by linking them to the grid used by POM. Estimates of territory size and overlap can then be used in POM to estimate abundance at both the state level and finer spatial scales (e.g., within each MFWP region).

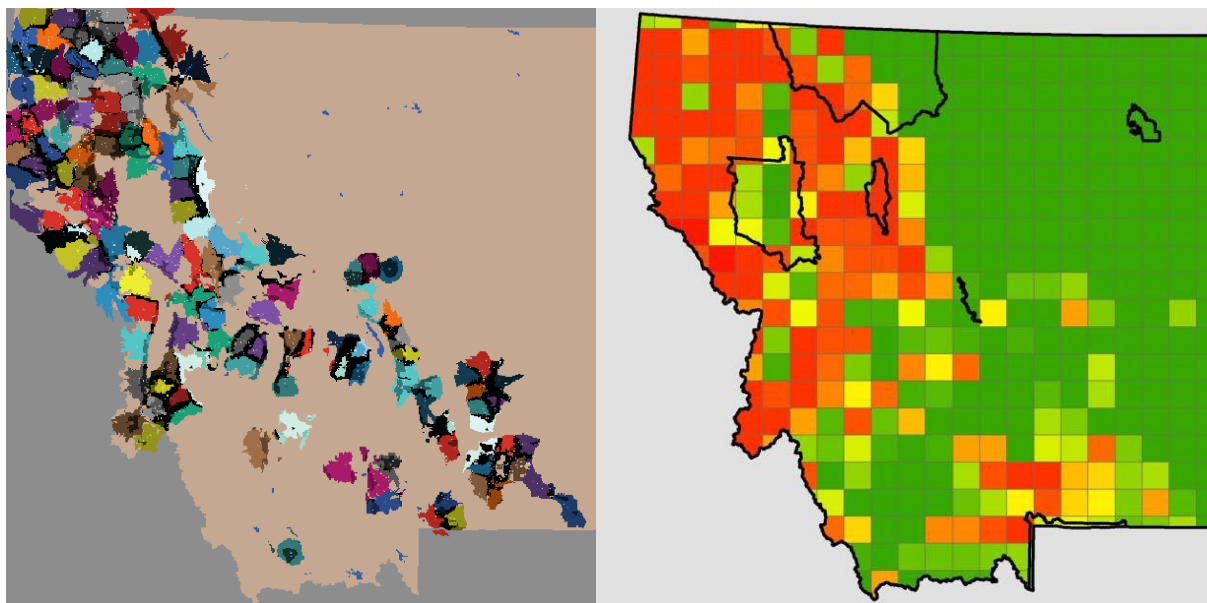


Figure 2.12. At left, a demonstration of the spatial predictions that can be generated in phase three of the territory model. Patches not part of territories are brown (or blue, where there are large lakes or reservoirs). Agents and their territories (representing different packs) range in color. Black patches between territories indicate overlap. We will compare how well real wolf territories and occupancy estimates for Montana align with model predictions from POM (at right; red indicates highest occupancy probability, green lowest).

The territory model's estimates will also be incorporated into the adaptive harvest management model (Study Objective #3) to predict future abundance of packs if various management actions were implemented. Results from the territory models will demonstrate how territorial behavior and total abundance could potentially be affected, e.g., by manipulating the distribution or abundance of ungulates, or increasing or decreasing harvest pressure (e.g., through higher or lower bag limits).

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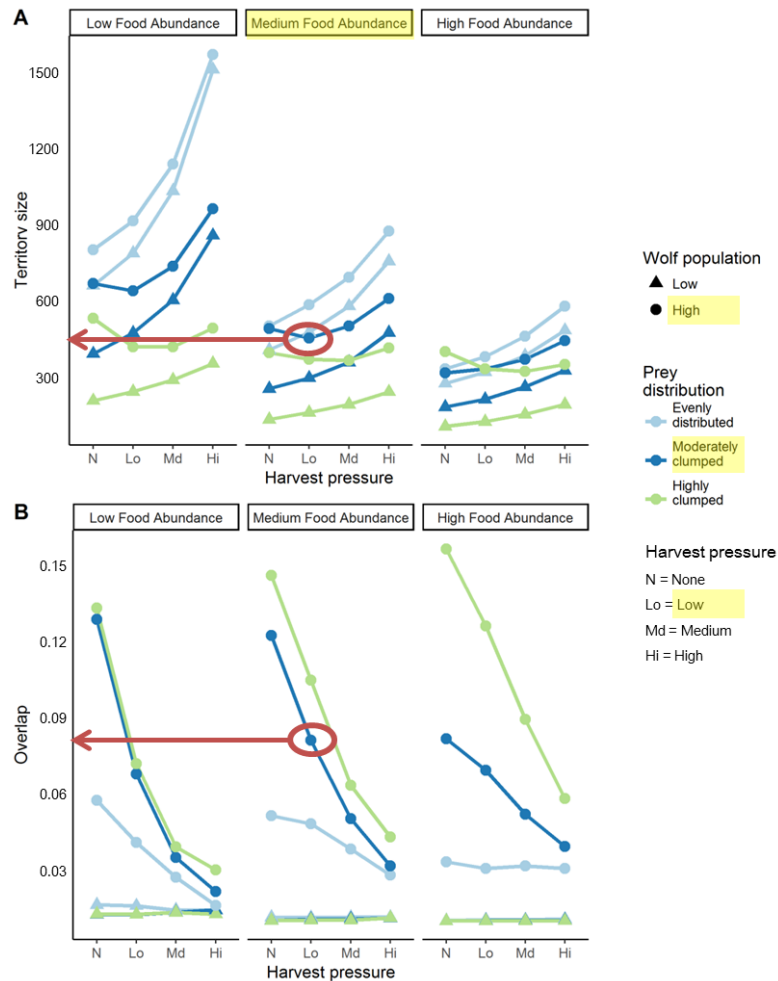


Figure 2.13. Illustration of the type of figures that will be derived from phase three of the territory model. This can be used to calibrate estimates of territory size in POM. For example, if within a given region, it was estimated that the wolf population was on the relatively high side, prey were relatively clumped and at moderate abundance, and harvest pressure was low (red circles), territory size and overlap could be estimated accordingly (red arrows). Figures will be prepared through final simulations of territory selection by wolves in Montana.

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APPENDIX A. THEORETICAL TERRITORY MODEL SELECTION ALGORITHM

For each simulation, the model cycled through a series of processes (Fig. 2.4) through which territories and competition among agents emerged on the landscape, as follows:

1. Setup landscape: a landscape configuration, threshold of resources (V_T), and patch-value algorithm (below) was specified.
2. Start new agent: a new agent A_i was added to the landscape and encountered resident agents A_R (those with territories; $\Sigma A_R = 0$ when a simulation began). An $\Sigma A_R = 10$ represented a low density population.
3. Pick territory center: A_i was moved to the patch with the highest center value index (V_{index}). A patch n 's $V_{index} = 0$ if any patches in radius ≤ 4 were owned by competitors (approximating the cumulative cost of competition likely to be encountered nearby; Sect. 2.4); otherwise V_{index} was the sum of the approximate value of patches $1 - x$ in radius $V_T \times 0.15$:
$$V_{index} = \sum_1^x B - D \times 0.01 - P \times 0.1$$
where D was the distance of patch x from patch n .
4. Calculate patch values: the value of each patch (V_n) relative to A_i 's territory center was determined using the patch-value algorithm (details below) defined in Process 1.
5. Establish territory: patches were added to A_i 's territory in order of V_n until $\Sigma V_n \geq V_T$.
6. Check center: if A_i 's current territory center \neq the territory's geographic center (i.e., \bar{x} and \bar{y} coordinates of A_i 's patches), A_i 's current territory was discarded, A_i was repositioned to this geographic center, and proceeded from Process 4. If the territory center = its geographic center, A_i proceeded to Process 7.
7. Summarize territory: A_i 's territory size (total space used, i.e., # of patches selected + travel corridors to selected patches), overlap (proportion of the selected territory shared with >1 agent), competitor pressure (ΣA_R at territory establishment), and the landscape's territory abundance was calculated.
8. Assess territory overlap: details about increases or decreases in overlap with neighbors was assessed and stored for each A_R , until it was their turn to proceed to Process 9.
 - a. If any agents remained queued, one agent proceeded to Process 9 as the new focal A_i .
 - b. If no agents remained queued,
 - i. if the landscape was not saturated (sufficient resources remained for additional agents to form territories), Process 2 was initiated.
 - ii. if the landscape was saturated, Process 10 was initiated.
9. Update territory: the new focal A_i 's territory was discarded and A_i proceeded from Process 4 to account for changes in the cost of competition imposed by neighbors. A_i 's territory was shifted if patches formerly selected had become uneconomical, or patches formerly ignored had become economical (e.g., due to < competition for those patches). Effects of competition were thus dynamic (i.e., changing continuously throughout a simulation) and density dependent.
10. End simulation: once the landscape was saturated (e.g., Fig. 2.5), the simulation ended. Final territory size and overlap was recorded for A_R , representing the results at a saturated population

density. The total abundance of territories was recorded, representing the landscape's carrying capacity.

We designed 2 patch-value algorithms for use in Process 4. During territory selection, all agents used the same algorithm to assess V_n :

$$A_B \text{ (representing } H_B\text{): } V_n = B - C_\Sigma - T_\Sigma.$$

$$A_P \text{ (representing } H_P\text{): } V_n = B - C_\Sigma - T_\Sigma - P_\Sigma.$$

V_n was the benefit of food (B) on patch n discounted by cumulative costs to reach it, representing the average costs that would be encountered to reach patch n from any patch in the territory (Mitchell and Powell 2004):

1. Cumulative cost of competition (C_Σ): because competitors are more likely to be encountered with each patch trespassed and likely to respond more aggressively the further inward a trespasser intrudes (Vines 1979; McNicol and Noakes 1981; Giraldeau and Ydenberg 1987; Eason 1992; Adams 2001), C_Σ was the local cost of competition (C_{local}) accrued between A_i 's territory center and patch n :

$$C_\Sigma = \sum_1^n C_{local}, \text{ where } C_{local} = N_{territories \text{ claiming}} \times 0.1,$$

where $N_{territories \text{ claiming}} = \#$ of other territories claiming the patch.

2. Cumulative cost of travel (T_Σ): T_Σ accounted for D (the # of patches between the territory center and patch n):

$$T_\Sigma = D \times 0.01.$$

3. Cumulative cost of predation risk (P_Σ): P_Σ was the sum of the local cost of predation risk (P_{local}) between A_i 's territory center and patch n , representing the increased chance of encountering predators for each patch crossed with predation risk:

$$P_\Sigma = \sum_1^n P_{local}, \text{ where } P_{local} = P \times 0.1.$$

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OBJECTIVE 3: DEVELOP ADAPTIVE HARVEST MANAGEMENT FRAMEWORK—*Allison Keever, Project 2*

3.1 Introduction

Harvest is an important management tool for gray wolves in Montana. Harvest regulations for wolves are evaluated biennially and can be updated as needed dependent on the status of the population and objectives for management. Decisions on harvest regulations for wolves can be challenging, however, due to conflicting objectives from various stakeholder groups and uncertainties in the effects of harvest on wolf population dynamics.

Conflicting opinions on values of wolves and management among stakeholders (including livestock producers, hunters, tourists, and wolf conservation groups) make management decisions difficult. Federal and state agencies have legal requirements to manage the wolf population, and the Commission-approved Montana Wolf Conservation Strategy stipulates that MFWP will maintain a minimum of 15 breeding pairs and 150 wolves to have a regulated, public harvest season. Ungulate hunters have concerns that wolves affect prey populations and compete with hunters for ungulates (Ericsson and Heberlein 2003). Livestock producers can suffer losses due to depredation events. Wolves also benefit the tourism industry (e.g., visitors to the region to view wolves), and conservation groups use that information to demonstrate the economic benefit of wolves (Defenders of Wildlife 2013).

A further challenge in managing wolves is uncertainty in effects of harvest on population dynamics. This uncertainty can stem from 2 factors. First, managers cannot directly control harvest rate, because changes in harvest regulations do not directly change harvest rates. For example, increasing the bag limit from 1 to 5 wolves does not mean that harvest rate would increase five-fold, or even at all. Harvest rates vary based on many factors, including weather, hunter and trapper effort, hunter and trapper success, and regulations. Second, there is uncertainty in the effects of harvest on demography. There is not consensus for how harvest affects wolves (Fuller et al. 2003; Adams et al. 2008; Creel and Rotella 2010; Gude et al. 2012). Substantial variation occurs in the reported level of harvest wolf populations can sustain before growth rate decreases (Fuller et al. 2003; Adams et al. 2008; Creel and Rotella 2010; Gude et al. 2012) which could result in management actions not reaching objectives.

Despite uncertainty in the effects of harvest and the conflicting objectives and values of stakeholders MFWP must still make recommendations for harvest regulations of wolves. This can be challenging, however, without a formal process.

Adaptive harvest management (AHM) provides a framework to clarify decisions while reducing uncertainty to identify the optimal strategies to meet objectives (Walters 1986, Williams et al. 2009). AHM is an extension of structured decision making (SDM; Hammond et al. 1999) when decisions are iterated over time or space and outcomes are uncertain. Much like SDM, AHM requires clearly defined objectives, alternative management actions, and a model to predict outcomes of actions and evaluate tradeoffs. An essential component to AHM is a monitoring program to determine the system state (e.g., population size), reduce uncertainty, and learn over time. Learning is the reduction of uncertainty and occurs when there are multiple hypotheses about how a system works, represented as multiple models

each with some probability of being the best model. These model probabilities can be updated by comparing model predictions to monitoring data and provide evidence in favor of a hypothesis over others. When a hypothesis gains support, uncertainty is reduced and the updated models can be used to make predictions. Future decisions can be improved because the updated models would be more predictive.

3.2 Sub-Objectives of Objective #3

To address the challenges associated with managing wolves in Montana we will develop an AHM framework that relies on meeting 4 sub-objectives:

1. **Collaborate with MFWP to determine their objectives and alternative harvest regulations.**
2. **Evaluate relationship between harvest regulations and rate.**
 - a. Improve understanding of variation in harvest rate.
 - b. Account for uncertainty in relationship between harvest regulations and rate.
3. **Incorporate POM (Study Objective #2): Predict abundance under alternative harvest regulations.**
4. **Develop AHM framework.**
 - a. Determine optimal harvest strategies.
 - b. Reduce uncertainty.

Meeting these sub-objectives (with Study Objectives #1 and #2) will contribute to meeting Study Objective #4, developing a targeted monitoring program.

3.3 General Approach

Our goal is to develop an AHM framework for wolves to help inform current decisions while reducing uncertainty in the effects of harvest to improve future decisions. AHM follows a general cycle: 1) Determine optimal harvest strategies dependent on objectives, alternatives, current status of the population, and the competing models (hypotheses) and their associated model probabilities of being supported, 2) Enact optimal harvest strategy (or another option following evaluation of tradeoffs), 3) monitor changes in population size, and 4) compare

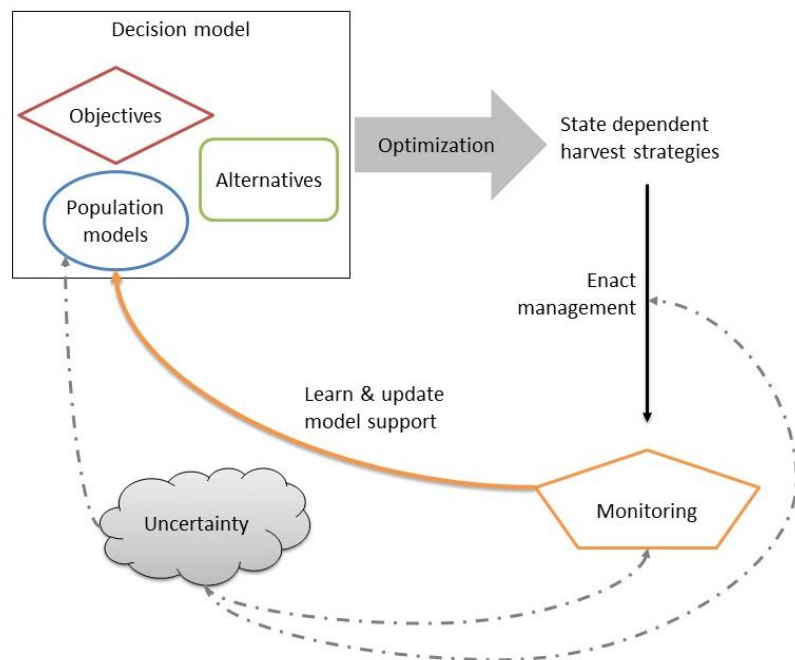


Figure 3.1. Adaptive harvest management cycle. The optimal state-dependent (i.e., population size dependent) harvest strategy is based on objectives, alternatives, the population models, and their relative support. After management is enacted, the response of the population is monitored and compared to predictions from the population models. Based on comparisons, model support is updated and uncertainty reduced.

monitoring data to model predictions to update model probabilities. The cycle then continues again (Figure 3.1).

Work is in progress to determine objectives and alternative harvest regulations with MFWP (detailed below). We will have draft objectives and alternative harvest strategies by April 2019.

3.4 Objectives and Alternatives

Introduction

Objectives for wolves were developed by MFWP representatives during a structured decision making (SDM) workshop in 2010. The working group focused on including objectives of the different stakeholders. These objectives included:

1. *Maintain positive and effective working relationships with livestock producers, hunters, and other stakeholders*
2. *Reduce wolf impacts on big game populations*
3. *Reduce wolf impacts on livestock*
4. *Maintain hunter opportunity for ungulates*
5. *Maintain a viable and connected wolf population in Montana*
6. *Maintain hunter opportunity for wolves*
7. *Enhance open and effective communication to better inform decisions*
8. *Learn and improve as we go*
9. *Increase broad public acceptance of harvest and hunter opportunity as part of wolf conservation*
10. *Gain and maintain authority for the state of Montana to manage wolves*

Methods

These objectives have been guiding management decisions for wolves since 2010 and have been adopted by the Montana Fish and Wildlife Commission as part of every public harvest season since that time. To determine if these objectives describe what is most important for wolf management in Montana, we met with MFWP supervisors, wildlife managers, wolf specialists, and regional biologists September 2018 and January 2019 (Table 3.1).

We asked attendees whether stated objectives captured what was important for wolf management and were still relevant. We documented opinions and revisions of existing objectives and documented new objectives.

There were several alternative actions proposed for wolf management.

Table 3.1. Dates, locations, and attendees for each of the regional meetings to discuss objectives and alternative actions for wolf management.

Region	Date	Location	Attendees
Region 1	11/2/18	Kalispell, MT	N. Anderson, D. Boyd, T. Their, T. Manley
Region 2	10/18/18	Missoula, MT	M. Thompson, B. Jimenez, E. Bradley, T. Parks, J. SunderRaj, R. Mowry, S. Eggeman
Region 3	10/29/18	Bozeman, MT	H. Berk and B. Inman
Region 4	9/26/18	Great Falls, MT	G. Taylor, B. Lonner, R. Rauscher, and T. Smucker
Region 5	1/8/19	Billings, MT	A. Nelson, M. O'Reilly, A. Taylor, B. Beck, S. Stewart, T. Smucker, J. Paugh, and K. Kembel
Region 6	9/27/18	Glasgow, MT	S. Thompson and M. Sullivan

Method type (rifle, bow, and trapping), season length (for each method or total), hunter and trapper permits, and the number and location of wolf management units (WMUs) have been proposed, however other actions may be included after further collaboration. We asked attendees their opinions and revisions to the harvest regulations along with 2 hypothetical questions to determine if existing regulations were sufficient: 1) if the population was low then how would you change regulations to increase the population, and 2) if the population was high how would you change regulations to decrease the population.

Preliminary Results and Discussion

The objectives that were developed in 2010 appear to still capture what is most important for wolf management and what is perceived to be important to the various stakeholders. We will finalize a draft of objectives and alternative regulations with MFWP by April 2019.

Overall, attendees in the different regions believed the objectives developed in 2010 for wolf management were still appropriate. Minor edits/rewording and the addition of a few objectives were suggested. The additional objectives mainly focused on values of non-consumptive stakeholders. We highlight some examples below.

It was suggested that objectives 2 (*reduce wolf impacts on big game populations*) and 4 (*maintain hunter opportunity for ungulates*) were related and could be reworded and combined. It was also suggested that objective 6 (*maintain hunter opportunity for wolves*) be updated to include trapping, or be combined by saying “harvest.” There were similar minor edits suggested for other objectives as well. Suggested rewording for objective 9 (*increase broad public acceptance of harvest and hunter opportunity as part of wolf conservation*) was to focus more on conservation and management in general: *increase public acceptance of wolf management and conservation*.

Overall, attendees believed that the harvest regulations available (e.g. permits or season length) were sufficient for management. No new tools were suggested to supplement those already available. In general, changes to season length and number of permits were suggested to alter harvest rate.

3.5 Next Steps

After the 2018-2019 harvest season for wolves is complete, we will begin work on sub-objective 3. Harvest rate is dependent on hunter and trapper effort and success. Effort and success could be affected by many factors, including method type, season length, distance to roads or road density (Person and Russell 2008), amount of public, weather, or land cover type. We will build predictive models of harvest rate based on data of hunter and trapper effort and success rate using linear models (e.g., GLM or GLMM) in a Bayesian analysis to determine a posterior distribution of harvest rate dependent on regulations. The posterior distribution of harvest rate can be used instead of using a constant harvest rate based on regulations to account for uncertainty.

We will use the objectives and alternatives from sub-objective 1 and POM, territory models, and group size models (Study Objective #2) in the AHM framework. POM will be used to predict the wolf population response to harvest regulations under multiple hypotheses represented as competing models. We will posit hypotheses of how harvest affects occupancy, territory size, or group size (based on Study

Objective #2), and the competing models and associated uncertainty with estimates can be reduced over time. Therefore, the harvest model from sub-objective 3 will be used to predict harvest rate given regulations. Outputs from POM includes number of wolves and number of packs which will be used to determine the effect of the harvest regulations on meeting objectives (after objectives are completed).

Monitoring should focus on the critical uncertainties that impede effective management. In some instances, reducing uncertainty does not affect decisions (e.g., Smith et al. 2013), and may not be worth the cost of collecting the data. The expected value of information (Raiffa and Schlaifer 1961; Runge et al. 2011; Williams et al. 2011), which represents the increase in effectiveness of management expected if uncertainty were reduced, can be used to help prioritize monitoring efforts. We will conduct a sensitivity analysis (Clemen and Reilly 2001) to determine the influence of model components on the harvest decisions. We will also use the value of information (Raiffa and Schlaifer 1961) to determine the uncertainties to reduce to improve management decisions. This and models and results from Study Objective #1 and #2 will allow us to design a targeted monitoring program.

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